XIII. THE LIFE-HISTORY OF THE COMMON WATER-NEWT (NOTOPHTHALMUS VIRIDESCENS), TOGETHER WITH OBSERVATIONS ON THE SENSE OF SMELL.

By Philip H. Pope.

(Plates XLI–LI.)

Introduction.

After such exhaustive papers as those of Gage ('91b)* and E. C. Jordan ('93) further work upon the life-history of this animal might seem superfluous. However, during several years of collecting and study of various Urodeles I have come upon a number of facts, which are either new, or have been incorrectly interpreted by earlier writers. These observations are based on collections made in Maine, New Hampshire, New York, New Jersey, Pennsylvania, and Illinois, and on experimental work carried on at Harvard during the years 1916 and 1917, continued at the University of Pittsburgh in 1919, 1920, and 1921, and concluded at Cold Spring Harbor in the summer of 1921.

I take this occasion to acknowledge my indebtedness to Dr. Manton Copeland, who first suggested the work on this species; to Dr. G. H. Parker, under whose direction it was first undertaken; to Dr. L. E. Griffin, Dr. and Mrs. H. H. Wilder, Prof. H. D. Fish, Dr. H. H. Collins, and Miss Louise Smith for their valuable advice and suggestions; and to Prof. H. E. Fernald, Miss Louise Smith, and Miss Elnora Lawson for specimens. I wish also to express to Dr. C. B. Davenport, my appreciation of the privilege of working at the Biological Laboratory of the Brooklyn Institute of Arts and Sciences at Cold Spring Harbor, and of the many courtesies extended to me while there. To Dr. W. J. Holland I am indebted for the editorial revision of these pages and for seeing them through the press.

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* The citations in parentheses refer to the Bibliography at the end of the article.

Part I. LIFE-HISTORY.

The purpose of the first part of this paper is to state the known facts in the life-history of *Notophthalmus*, combined with such original contributions as I have been able to make, and also to suggest further work on points which as yet are not clear.

Gage ('91a) quoted below, has summed up the main facts in the life-history. He says: "I have now demonstrated the following facts with reference to this amphibian:

1. The eggs are internally fertilized;
2. The larvæ have the form and coloration of the adult aquatic form;
3. When the gills are lost, the animal becomes terrestrial, and changes its viridescent color for red;
4. At maturity the red terrestrial form goes into the water and assumes a viridescent coloration;
5. In aquatic forms, whether adult or larval, the epithelium of the mouth is stratified and non-ciliated;
6. In the terrestrial forms, the oral epithelium is ciliated."

Most of the facts in this statement still remain unquestioned. Earlier writers have placed the terrestrial form in a separate species, and some believed it to belong to a separate genus. Gage ('91b) offered such conclusive proof of the unity of the two forms that the fact has never since been doubted.

Gage's annotated bibliography is so complete, that it seems hardly necessary to review the work of the earlier writers.

Jordan ('93) has written an excellent account of the natural history of *Notophthalmus*. His description of the breeding habits, including the egg-laying and the anatomy of the reproductive organs, is especially good. In the main his conclusions are similar to those of Gage, though rather more detailed and accurate in some particulars. The greater part of Jordan's paper is taken up with the maturation, fertilization, and early development of the egg, ending with the formation of the notochord. This subject is not within the scope of the present paper.

1. BREEDING HABITS.

Breeding Season. *Notophthalmus* begins to breed early in the spring and continues until early in the summer. In Maine I have found it mating in early April, soon after the ice left the pools. In western Pennsylvania fifty specimens were collected on March 23, 1920, in a large pool, where they were mating freely. The females in this lot laid eggs in the laboratory March 30.

Unlike the frogs and *Ambystoma*, the breeding season of *Notophthalmus* is quite extended. Jordan ('93) writing of conditions at Worcester, Mass., says: "Egg-laying begins about the tenth of April and is brisk until the first of July. It is probable that for a single individual the egg-laying season lasts for at least seven or eight weeks." Near Pittsburgh my earliest record of egg-laying was March 30. In 1920 and 1921 the newts continued laying until the second week in June, when my departure stopped further observations.

Mating Behavior. In the breeding season, the stout hind legs of the male develop black, horny pads on their inner surfaces. Under the microscope these are seen to consist of a layer of thickened cells, each of which bears a conical point. They suggest the pads on the thumbs of such frogs as *Rana pipiens*, which serve the same purpose. At the same time the tail of the male increases in width until it is fully twice as wide as that of the female, while the thin edges have a wavy appearance because they are longer than the main part of the tail. At this season, the sexes are very easily distinguished by the characters mentioned and also by the larger size and plumper body of the female. Figs. 1 and 2 (Pl. XLI) will illustrate some of these sexual differences.

The male seizes the female around the neck or anterior portion of the body with his hind legs and clings tenaciously for half an hour or more. The female is usually quite passive, remaining quiet, with legs outspread, body straight, and tail curved upward. The male, on the other hand, is very much excited. The cloaca is widely opened and pressed against the back of the female, showing a fringe of villi. The tail is generally curled around parallel to the body and is constantly waving and twitching. The body is doubled up and the side of the head pressed or rubbed against the snout of the female. This position is frequently changed, so as to bring the other side of the head against the nose of the female. After the male has retained his hold for some time, he begins to shake the female violently and to drag her all around the place. This seldom lasts for more than a few minutes at a time, and it is usually during one of these paroxysms that the male finally shakes himself loose. Jordan ('91) has given us the best account of mating that has yet been published. He says that after the male leaves the female he does not go far, but remains on the bottom near by, with cloaca still everted and body twitching. If the female follows him and touches his tail or cloaca, he is stimulated to deposit a spermatophore. The spermatophore consists of a transparent basal disc of jelly-like substance, having on its upper surface a tapering stem with a conical base surmounted by a white ball of motile spermatozoa. The base is 8 or 10 mm. in diameter, and the stalk rises above it to half that height. The disc is more or less loosely attached to the bottom so that the sperm mass is held up into the water on the slender tip of the stalk. This is well illustrated by Jordan ('93, Plate XIV, fig. 2).

The spermatophore is not always of the typical shape just described. One, which I saw, consisted of an irregular lump of jelly, bearing a single conical point, where a mass of sperms had evidently been detached, and several shorter points sticking out in different directions. A mass of sperms was completely imbedded in the jelly where it could hardly have been functional. The female seems to get the spermatophore by following the male and bringing her cloaca over it. From this it would seem that fertilization must be largely by accident, although Jordan believes that the glands of the cloaca in the female secrete a substance which has a chemical attraction for the sperms. Jordan ('91) says that the male may deposit three spermatophores, but seldom more. If fertilization were wholly dependent upon the spermatophores, it would seem very uncertain, in spite of several matings in a season; but Gage ('91b) has shown that the motile sperms escape freely into the water. If there is real chemical attraction, it seems likely that many of these sperms find their way into the cloaca of the female and effect fertilization without spermatophores. It is certain that the female does not always follow the male, but comes to the surface for a breath, or swims away quite regardless of him.

Some careful experiments on chemotaxis ought to show whether there is really a chemical attraction to draw the sperm into the cloaca of the female. As in most Urodeles, the sperm is stored by the female in sacs opening on the dorsal wall of the cloaca. These sacs have been variously named. Jordan speaks of the "*receptaculum seminis*," referring to all the sacs as one organ; while Kingsbury prefers to call them spermathecas or merely tubules.

Jordan ('93) has summed up the literature on the *receptaculum seminis* of the female, and seems strongly inclined to believe that the epithelium lining the sperm-sacs has a secretory function to attract the sperm which is stored in these sacs after mating. Kingsbury ('95), who has sectioned and studied the spermathecæ, also believes in the chemotaxis theory. His description of the spermathecæ follows: "They are flask-shaped, the neck is constricted and the diameter of the body of the cul-de-sac varies with the amount of distention caused by the zoösperms contained. The shape of the lining cells was also modified by the same cause; in the empty tubules, however, they were cubical. Each tubule is enclosed in a layer of plain muscular fibers which encircle it. The tubules open upon the lateral walls of the dorsal extension of the (cloacal) cavity, which is divided into two parts by the mesal elevation."

Kingsbury puts the total number of spermathecæ at about fifty-five, each capable of containing large numbers of spermatozoa.

Jordan ('91) has had a female lay ninety-six fertilized eggs after separation from a male, the last of which were laid nineteen days after her isolation. He believes that a single mating in a season is all that is necessary to fertilize all the eggs which will be laid for that year, which seems very probable in the light of Kingsbury's work on the anatomy of the spermathecæ.

Fertilization. Jordan ('93) describes the function of the spermathecæ. He says: "The fertilization of the egg takes place just before the egg is extruded. The spermatazoa, which have long been in waiting in the tubes of the *receptaculum seminis*, are either attracted from their resting places by the passing egg, or forced out by contraction of the surrounding muscles. I have made repeated and careful search for spermatazoa in the oviducts, but have never succeeded in finding one. Neither have I ever found in sections any indication that spermatazoa enter oviduct eggs, although eggs often lie for some time in the mouth of the oviducts. Fertilization, then, would seem to take place only after the egg has left the oviduct and passed into the cloaca."

From the fact that unfertilized eggs are often dropped by females in captivity, and that these eggs are not laid on leaves, but escape into the water, Jordan concludes that the spermatozoa are normally passed out of the spermathecæ during the act of oviposition. It seems probable that this is the function of the smooth muscle fibers, described by Kingsbury ('95) surrounding the spermathecæ.

Jordan also says that the egg is held in place by the sticky secretion poured out of the cloaca. It seems likely that the origin of this secretion is to be found in the tubular pelvic glands, which lie ventral to the spermathecæ.

The purpose of the male in rubbing his head against the female's nose is to stimulate her with the secretion of the glands in the side of the head, thus causing her to follow him.

On the side of the head of the male are three or four shallow pits behind the eye and at a level with it. Of these the hindmost, located on the mass of muscle above the angle of the jaw, is flat-bottomed and slightly crescent-shaped, and about 0.5 mm. in diameter. Hilton ('02) has sectioned and studied these pits. He finds that they are generally present in rudimentary form in the female, making their appearance at about the time that the red form enters the water. In the male they appear earlier, at about the time that the sex can be determined by gross dissection. The pits in the adult male are lined with simple saccular glands, which in turn are lined with columnar epithelium. In the breeding season the glands are greatly enlarged, the fundus becoming filled with secretion and the cells growing shallower, approaching the cubic, rather than the columnar form. So far as I know, no bio-chemist has studied the nature of this secretion. It would be interesting to secure a little of it and note its effect upon an isolated female.

Several males often gather about one female. Jordan ('93) reports finding as many as ten or twelve males thus congregated. He has noted the fact that the males considerably outnumber the females. Among four hundred and twenty-six specimens, he found two hundred and eighty males. My records show a still larger percentage of males: three hundred and thirty-nine out of four hundred and thirty-five. These figures respectively give 65 per cent. and 77.9 per cent. of males. Nevertheless it seems doubtful whether the sex ratio is as unequal as shown by these observations. I should like to know when Jordan collected his newts. Most of mine were taken in the months of

March, April, and May, when they were breeding freely, and a few in November and December, when the fall mating season was on. At such times I believe the males are much more active and conspicuous than the females, and their habit of gathering about one female would render them far more liable to capture. It is my belief that during the breeding season the females are quiet and inconspicuous, except when they are actually mating.

Jordan's specimens were probably taken at all seasons, which would account for the smaller percentage of males. I would like to compare the sex ratio of a large series taken in July or August, or the complete census of a drained pond with the figures given above, for I feel sure that it would show a larger percentage of females.

Toward the end of the breeding season, the males lose the sexual characters, which make them so conspicuous, and for the rest of the summer they can hardly be distinguished from the females. A lot of ninety-six collected in Sunderland, Mass., June 15, 1921, while the females were still laying eggs, contained no conspicuous males and many individuals of doubtful sex. It is my belief that the pits on the sides of the head in the male, would always serve to distinguish the sexes, but I have not taken time to work this out.

Laboratory conditions often check breeding activities. On March 23 and April 1, 1920, I collected two lots of newts. The first lot began to lay eggs March 30, and the second lot as soon as captured. On April 17 oviposition had decidedly fallen off, and on the 23rd it had ceased entirely in two out of my three aquaria. At this time the males had lost the black pads on the hind legs and the feather-edge on the tail and there was very little mating activity. I believe that temperature is the most important factor in this decline. In the pools at this time of year it varied from 13.5° to 21.5°C, and in the laboratory, from 20° to 24°C. Jordan ('93) found that animals kept over winter in the laboratory would seldom lay eggs in the spring. My own experience agrees with this, and I believe that temperature is the chief reason.

The curious phenomenon of mating and deposition of spermatophores in the fall has been recorded by both Gage and Jordan, but neither is able to account for it. I have observed it both in the field and the laboratory, but can see no real explanation. The fact that no eggs are laid in the fall seems to make it quite superfluous. I believe, however, that it is merely a preliminary to the spring mating season. Gage says: "In the autumn the males will be found to possess the dark, horny toe-tips and ridges on the thighs. . . . and the tail will be found as fully developed as in April."

On Dec. 3, 1920, I collected one female and five males near Pittsburgh. Mating was taking place in the laboratory Dec. 9, and I isolated the pair. The next day they mated twice, but I was unable to find any spermatophores either time. All of the males captured at this time had the sexual characters mentioned by Gage fully developed. This leads me to think that these characters are retained throughout the winter, and that mating begins in the fall, being interrupted only by the period of inactivity due to cold weather, and beginning again in the spring, as soon as the temperature of the water begins to rise. Newts left in the laboratory will continue mating all winter to some extent, though not as actively as when first captured. I have also seen mating in the middle of July after the usual mating season was over.

If a portion of a natural pond could be screened and the normal activities of a few of the animals watched daily for an entire year, a great many doubtful points might be cleared up.

Ovulation. When laid, the egg has the shape of a sphere, or oval, about 1.5 mm. in diameter, the outer part consisting of a firm and somewhat milky layer of albumen with the egg proper in the center. This is spherical and about one-fourth of a millimeter in diameter. The albumen is much firmer than that of frog's eggs and does not soften and expand during the development of the egg. The membrane covering the outside is not sticky to the touch, but, when first laid, it adheres so firmly to the leaves that it must usually be torn to dislodge the egg.

The manner in which the egg is fertilized has been mentioned in connection with the function of the spermathecæ. The eggs are usually laid singly on the leaves of water-plants, although occasionally two, or even three, are laid on the same leaf. *Notophthalmus* usually selects some plant with thin, flat leaves, which can be folded readily to conceal the egg, although such plants as *Myriophyllum* or *Cabomba* may be used, if no others are available. The following description of the egg-laying process is from Jordan ('93): "She then bestrides the chosen spray of water plant and gathers in with her hind legs the surrounding shoots, pressing them close around her cloaca. She next turns on her side or occasionally on her back, and with forelimbs outstretched and rigid, with hind limbs and twigs completely hiding her cloaca, usually remains perfectly motionless for about six to eight minutes. At the end of that time she slowly leaves the 'nest' which now holds an egg, well protected by the tangle of shoots glued together by the gelatinous secretion poured out of the cloaca."

I have found the eggs in a pond near Pittsburgh on the leaves of *Ludwigia*, *Proserpinacea* and an aquatic species of *Polygonum*. The egg is either placed in the axil of a leaf or the leaves are gathered around it and stuck together; or more often the leaf is folded and the egg laid in the fold, its gelatinous covering holding the leaf in place. In one of my aquaria, I have seen a long leaf of *Polygonum* folded three times with an egg in each fold. Figs. 3 and 4, (Pls. XLII and XLIII) show something of the manner in which the eggs are laid. In this way the eggs are well hidden and protected from natural enemies. I have seen an adult *Notophthalmus* try repeatedly to eat an egg surrounded by the leaves of *Myriophyllum*, but the plant yielded and the lunges made by the newt only pushed it away.

2. DEVELOPMENT OF THE YOUNG.

Development of the Egg. The embryology of *Notophthalmus* does not come within the scope of this paper. Jordan has given a very full account of the formation of the egg and its development up to the time of the formation of the neural groove. It remains for some other investigator to take up the further development of this animal.

Gage ('91b) says: "The eggs hatch in from twenty to thirty-five days, depending on the temperature."

In the spring of 1920 I first found eggs in my aquaria on March 30. On April 11 the first one hatched; the second on April 13, and three more larvæ were seen on the 17th. This makes an incubation period of from twelve to eighteen days, instead of the twenty to thirty-five days set by Gage. He does not state where and at what temperature his animals were kept. Mine were in balanced aquaria at room-temperature, which probably hastened development somewhat.

Aquatic Larva. The larvæ are very small and not active at first. A description follows: Measurements, 8.5 mm. in length. Head nearly round, 1.5 mm. wide, nearly twice the width of the body behind the limb-buds. Balancers 1 mm. long. Gills a scant millimeter in length. Fore limb-buds elongated, sac-shaped structures. Hind limb-buds cannot be seen. The larva is slender, resembling a mosquito larva in general appearance. The tail is broadly finned, both dorsally and ventrally. The body is well pigmented, and especially the gills and tail.

The older larva is intermediate in appearance between the slender larva of *Eurycea* and the stout, broad-headed *Ambystoma.* The tail is very broad with a thin feather-edge both dorsally and ventrally. Ventrally this keel extends forward only to the cloaca, but dorsally it extends along the back as far forward as the base of the gills, narrowing gradually anterior to the hind legs. The tail has considerable power of regeneration. It is frequently bitten off by some natural enemy, or by other larvæ, and in a short time reproduces the missing tip. The limbs are slender and comparatively long. The toes of the fore and hind feet overlap, as the animal crawls.

The body is rather slender compared with *Ambystoma.* It is half or two-thirds as wide as the head, depending on whether the young newt is scantily or well fed.

The gills show the typical feathery, branched appearance, seen in most larval salamanders. In a larva 25 mm. long they measure about 3 mm. Like the tail, the gills frequently suffer from the greed of other young newts, and so they are often shortened, or even completely lost on one side. Regeneration is rapid, however, so that the loss does not seem to inconvenience the larva. One, which had all the gills of the left side completely bitten off, regenerated slender filaments 1 mm. long in two weeks.

The head is flattened dorso-ventrally. From the dorsal side the part between the eyes and the origin of the gills appears cylindrical. A line of dark pigment runs from the eye to the external nostril, making the snout appear more pointed than it really is. The head is so transparent that the outlines of the brain-cavity can be traced part of the way by the pigment in the lining of the cavity. A dark V can usually be seen with its legs pointing forward at the center of the eyes and its apex about 1 mm. in front of the origin of the gills. Sometimes a similar but inverted figure can be seen in front of this, forming a complete square. Just lateral to the angles of this square can sometimes be seen the silvery white otoliths. Several views of larvæ are shown in Figs. 5–14 (Pls. XLIV–XLVI).

Gage ('91a) wrote: "The larvæ have the form and color of the adult aquatic ones." This description fits the larvæ which have nearly completed their metamorphosis, but in the real larval stage, which lasts for three or four months, the coloration is quite different.

To the naked eye the young newt has a medium brown appearance with a slight tinge of green, flecked with very dark brown dots, and often showing a line of pale brownish spots along the sides above the lateral line. The under parts are immaculate white, instead of appearing yellow, spotted with black, as is the case before metamorphosis.

Under the binocular, the ground-color of the newt is seen to be pale green, tinged with lemon-yellow and thickly dotted with black chromatophores. This color is similar to that of the tadpoles of most frogs. It makes an admirable protective coloring for an animal which lives in pools having bottoms composed of mud. Like many other defenseless animals, the safety of which depends upon their invisibility, the young newts remain motionless most of the time. When they move, it is either in a very slow, crawling manner, or with a sudden and rapid dash to capture prey, or escape danger.

Food. *Notophthalmus* is carnivorous from the first. In my balanced aquaria I kept them in food by occasionally adding water from a culture of small crustacea such as *Cyclops*, and *Cypris*. I have seen larvæ actively chasing *Cyclops*, but more often they wait until the prey swims close by their noses and then snap it up instantly. A small larva captured Oct. 30, 1920, and sectioned the next day, had its stomach full of small crustacea. From this evidence I feel fairly safe in saying that crustacea form a large part of the food of the larva, although I imagine that no insect-larva small enough to be swallowed would be refused. In the laboratory they will eat finely chopped liver or earthworms.

From the fact that the larvæ will stay in *Spirogyra* when it is put into the aquarium, and that the algæ gradually disappear, I was led to believe that they sometimes varied their animal diet, but this was not proved until on Oct. 14, 1921, I put into the jar with my larvæ some one-celled green algæ and found that they eagerly gorged upon it. This alga grew in one of the ponds on the Reed College campus. I am not sure of the species, but think it belongs to the genus *Chlorobotrys*.

Duration of the Larval Stage. The average length of time spent in the larval state is about four months. In New England the eggs are laid from early April to early in July. In late July and August the larvæ can be captured by using a fine-meshed dip-net and dredging among the weeds. In the last week of August, larvæ, which have begun their metamorphosis, will be found; while by the middle of September, larvæ of all sorts are scarce, and those found are usually metamorphic. I have captured them in the true larval state as late as this in a cold, spring-fed pool, but could find none at all in the other pools where they had previously been abundant. Miss Smith ('20) has made collections at a later date.

The time of the change is a little earlier in the Pittsburgh region. On July 17 I collected ten larvæ that were not yet metamorphosing, but were fully grown. Some of them began their change in the laboratory on July 26. On July 31 I collected five more, of which three were already starting to change.

Unfavorable conditions, or other factors in environment, such as the cold water noted above, may delay metamorphosis considerably. Most of the newts hatched in my aquaria in 1920 changed in July. Two of them completed their change on June 28, while three delayed until winter. One of these began metamorphosis Jan. 21, 1921, and the last one completed its change March 18. Four larvæ hatched in the spring of 1921 remained in the larval state until late in the fall. Three of them metamorphosed Nov. 30, Dec. 9, and Dec. 15. At the present writing (Jan. 7, 1922) the fourth is still a typical larva. The fact that I captured a small larva near Pittsburgh on Oct. 30, 1920, shows that this sort of thing sometimes takes place in nature.

However much metamorphosis may be delayed, the larvæ never grow beyond a certain size before metamorphosis. The largest I have measured was 32 mm. in length. Gage ('91b) says: "The size attained before transforming is quite various. . . Indeed they may remain in the branchiate condition until they are as long as the adult aquatic ones, and two or three times the length of the red ones found in nature." I cannot agree with him on this point for the reason stated above, but must conclude that Gage confused the larvæ with those of some other species, possibly *Eurycea ruber* or *E. bislineata*, or perhaps *Gyrinophilus*, all of which may attain considerable size before transformation.

Metamorphosis. As the young larva approaches metamorphosis, the feather-edges of the tail begin to shrink until the tail becomes nearly round and is narrower than the body. At the same time the color undergoes change. The white abdomen begins to turn yellow and the back to darken and turn green, until at the completion of the change the general coloration is that of a dark specimen of the aquatic adult. The vermilion spots now appear on the back, though usually fewer in number than in the adult. The lungs develop, and the larva begins to come to the surface for air while it is still quite small, but the gills persist and apparently continue to function until the changes in the tail and in coloration are nearly complete. Then they begin to shrink at the tips until they become mere stubs and disappear entirely within two weeks. The remains of the gills lie down flat against the sides of the neck, showing as mere patches of black, thus completely covering the gill-clefts, which are closing up in the mean time.

The change in habits is as striking as the change in appearance. Instead of resting in the weeds, or actively searching for prey, the newly changed newt floats passively at the surface with its nose as far out as possible and its limbs sprawling into the water at random. Figs. 12, 13, and 14 (Pls. XLV and XLVI) show characteristic poses. If disturbed, the newt swims with difficulty and soon floats up to the surface again. It is no longer adapted to an aquatic life, and, when given the opportunity, will invariably crawl out of water and hide in moss or other shelter.

Figs. 5 to 15 (Pls. XLIV–XLVI) show practically all the stages of metamorphosis. Figs. 5 and 6 are slightly enlarged, but all the rest are of natural size, except Fig. 15, which is reduced a little. Figs. 5 to 9 inclusive are successive pictures of the same animal. Fig. 5 shows it as a typical larva, with broad tail, feathery gills, and the typical larval pattern even to the silvery white under-parts. Fig. 6 shows the general shape of head and body from the dorsal view. The narrowed base of the gills is quite characteristic. Fig. 7, taken six days later, shows how rapidly metamorphosis is taking place. The tail is narrow and the coloration practically that of the adult, but the gills remain nearly or quite of full size. A comparison of Figs. 7, 8, and 9 with Figs. 5 and 6 will, however, show a change in the gills. In the metamorphosing animal they seem to be slightly more bushy and to curl forward in a manner characteristic of this stage. This change of position is probably due to an antero-posterior degeneration in the epibranchial cartilages similar to that described in *Eurycea* (*Spelerpes*) by Miss Smith ('20a). These cartilages support the gills, and, as they become loosened from the rest of the hyobranchial skeleton during metamorphosis, they must allow much greater freedom of movement at this time. While I have not observed this process in this species, it probably takes place much as in *Eurycea*. Figs. 8 and 9, taken the next day, show little change, although a trace of the vermilion spots on the back can be seen.

Figs. 10 to 15 show successive views of other animals, covering the period between July 26 and Aug. 15, 1920. There were five animals in this lot, but owing to their activity, only three were ever successfully photographed on one plate. Fig. 10 shows a typical larva at the top, and at the left, a metamorphic animal in a characteristic pose, showing the narrowing of the tail. In Fig. 11, the typical shape of the larval head can be seen in the animal in the lower left hand corner. The uppermost of the other two shows a slight narrowing of the tail, while the lower one has completed this process and its gills have begun to shrink. Figs 12, 13, and 14 are given to illustrate late stages in metamorphosis. Fig. 12, photographed Aug. 1, shows but little change. The newt with its head at the surface still has traces of gills left. This Figure and Figs. 13 and 14 show the characteristic attitudes of the newly changed newt. The animal at the surface in Fig. 13 is in a typical pose. Fig. 14 very plainly shows the vermilion spots on the floating newt. It also shows one unchanged larva with the tip of its tail bitten off by one of its fellows. Fig. 15 is a dorsal view of two completely metamorphosed animals. All traces of gills are lost and the young newts look thin and emaciated. Their color at this time was similar to the adult, only darker dorsally. These animals had been out of water for ten days.

Just after metamorphosis, is the most critical stage in the life of young *Notophthalmi* reared in the laboratory. They may live for a while, but refuse food for some time, and generally die within a few weeks at most. Three months was the longest time that I ever succeeded in keeping one. If it had turned red in that time, I should have felt that the mystery of the color change was half cleared up.

Possibly the refusal to eat at first is due to structural changes in the mouth. Miss Smith ('20) has described the mechanism of a change in the hyobranchial apparatus of *Eurycea bislineata* at the time of metamorphosis. In that case the manner of capturing the prey changes from simply snapping it up with the jaws, to throwing the tongue well out of the mouth. *Notophthalmus* also changes its habits of feeding in a similar way after metamorphosis, for the land form can extend its tongue nearly an eighth of an inch to capture small insects.

3. TERRESTRIAL STAGE.

This is the most puzzling part of the life-history of *Notophthalmus.* The red newt was once placed in a separate genus and its identity with the water-newt was not fully settled until 1889, when Cope, following several earlier workers, stated that the red and viridescent forms were merely stages of one and the same animal.

It is not the purpose of the present paper to repeat Gage's admirable review of the development of this belief. It is my intention, however, to review carefully the evidence from which the conclusion was drawn. This consists of five main facts:

1. At the time of metamorphosis, the larva becomes terrestrial. Both Monks ('80) and Gage ('91b) have observed this fact and it agrees with my own observation.

2. The terrestrial form is not always red, but often approaches the viridescent coloration.

3. The terrestrial form has been known to change from the red to the viridescent coloration. This change may be induced artificially by keeping the newt in wet moss in the dark.

4. The terrestrial form is adaptable to aquatic life, with non-ciliated oral epithelium and aquatic respiration. Gage ('91b) says that this change comes when the sexual glands are mature, either in fall or spring.

5. The intermediate sizes between the aquatic larvæ and aquatic adults are not to be found in the water, but on land.

It will be noticed that while there is a large mass of evidence here, much of it is circumstantial. *Notophthalmus* has never been reared in captivity from the egg to the adult. That is not surprising, for this would require at least four or five years and constant care. The land-form has been adapted to water, but has never in captivity been induced to lay eggs, from which *Notophthalmus* larvæ have been reared. The larvæ often metamorphose in the laboratory, but, while they acquire the rounded tail and rough skin of the terrestrial form, they are always viridescent in color with yellow abdomens. It has been assumed, that, if kept long enough under the right conditions, they would turn red. This is probably true, but at this stage they are very hard to rear and always die within two or three months. The actual finding of the land form in its transition to the aquatic adult would complete the chain of evidence for the identity of the two species and also settle the question of the season when the newts return to the water.

Dr. H. H. Wilder has very kindly given me the following unpublished observations: "In Princeton, Mass., is a small ice-pond known as Echo Lake, where Notophthalmus was always very abundant. In the latter part of August, 1893, I found a great many newts along the wooded side of the pond, where the water was shallow. For a distance of at least 50 feet along the shore and from the land 10 feet out into the pond, newts were so abundant that one could hardly step without crushing one. These animals showed all possible shades of color, from the red woods form to the green aquatic adult. I collected 60 or 80, killed them, and laid them out on the table, arranged in a series which graded in two ways; first in color, as noted above, and secondly in roughness of skin, beginning with those that were so rough and dry that they repelled water, and ending with the smooth skin of the adult water-form. These two characters showed complete correlation in their variation, for the reddest animals had the roughest skin and the greenest ones were the smoothest."

In addition to this, Miss Louise Smith has sent to me forty-three newts collected on land and fourteen from the water at Williams Pond, Mt. Toby, Sunderland, Mass. on Oct. 2, 1921. Of these she writes: "Most of them were very near the Williams Pond and all of them were within a mile from there. . . . The color varies much more and approaches that of the aquatic adult much more closely than even the darkest of the little ones found far away from water, though many have a rusty tinge. One is scarlet and one a rich wine-color. We got some from the water too,—the brightest scarlet one of all was swimming around to his heart's content and there were many more that were not typical water adults.

"I feel convinced myself that at Williams Pond, Mt. Toby, Notophthalmus goes back to water late in September and early in October and a few stragglers early in the following spring. I think so, because we always find animals with a reddish tinge to a greater or less degree and rough skin, both in and out of the water at these times and no others, although we have not collected there in August."

The appearance and behavior of these animals, which Miss Smith sent to me alive, will be discussed later. The finding by two good observers of the land animals returning to the water supplies a strong link in the chain of evidence at one of the points where it was most needed.

The premises given above will be discussed point by point.

1. The description of the metamorphosis given on a previous page should suffice to prove that the larva always becomes terrestrial after the loss of its gills.

2. It is agreed that the animal loses its red color upon reaching maturity and going into the water, but it has usually been called a red animal while on land.

3. Several writers have observed the change from the red to the viridescent coloration, but none have seen a newt change from green to red in captivity. The green color seems to be associated with a damp, cool habitat, as in swamps or woods, while the reddest ones are found in hilly regions, usually at a distance from the water.

Several naturalists have induced the change from red to green by keeping the newts in wet moss or leaves for several weeks or putting them into the water.

Gage ('91b) has experimented with them and concludes by saying: "These experiments and observations seem to the writer to entirely preclude the notion that the red form owes its coloration to either food, season, or situation, but that it is normal for a given stage of its growth and development."

None of these workers has measured the animals with which he experimented. It seems probable to me, that, if Gage's conclusion is the correct one, a small newt could not be induced to change its color, but a large one that is almost ready to change would do so quite readily.

Gage also says that the change of color coincides with the maturity of the sexual glands and that at this time the animal will readily take to the water, if given the opportunity. In order to verify this point, I dissected seventeen land newts that were evidently about to re-enter the water. These animals were collected Oct. 2, 1921, by Miss Louise Smith, part of the lot which has been mentioned earlier. They were killed Oct. 26, and dissected later. The total length varied from 62 to 83 mm., the average being 77.11 mm. Three of these had the appearance of the ordinary aquatic form, and ten looked like the typical land form. The other four were intermediate in appearance. Upon dissection all were found to have well developed gonads. While the largest males had testes which were larger and showed the tubules more plainly than those of the smaller newts, the small males had sexual glands which were surprisingly large. One newt 70 mm. long had testes measuring 5 mm. in length. In the females also there seemed to be no clear correlation between the size of the animal and the state of development of the ovaries, although the ovary does not develop as early as the testis. The smallest animal in the lot had the smallest ovaries and the size of the individual eggs was only about half that of those in the large ones. Evidently the largest animals of both sexes would have become sexually mature the following spring, but it is hard to say whether all of them would have done so. In all of these animals the pits on the sides of the head could be seen, their size depending on the sex. In the male they were large and distinct, but in the female they were small and sometimes hard to find.

For comparison I also dissected seven smaller land newts collected at Branchville, N. J., in June, 1920, and kept alive for a month after that. These newts were all red and varied in length from 32 to 60 mm. In two males, measuring 54 and 58 mm. in length, the testes were respectively three and five mm. long, with a large, crescentic fat body curving around the ventro-median edge. In three females, measuring 60, 53, and 44 mm. in length, the ovaries were very small and the eggs microscopic, the whole organ being very small in the smallest animal. In the remaining two newts the gonads were too small to be found by gross dissection. None of these newts showed any sign of the pits on the sides of the head.

This evidence confirms what Gage says about the maturity of the sex glands at the time when the land form re-enters the water. From my dissection I should say that most and possibly all of the newts collected by Miss Smith would have become sexually mature the following spring. It is hard to account for the early growth of the testis in the male. An adult in the breeding season had a testis only 6 mm. long, as compared with 5 mm. in a young newt 58 mm. long, which was evidently only two years old. In the adult, however, the gland was plumper and would probably weigh twice as much. It also lacked the fat body that was so conspicuous in the young male. I do not believe that the large size of the sexual glands in the young male indicates that they resort to the water to breed and then take to the land again. If so, these small newts would be found with the older ones in the water during the breeding season and I should also expect to find the external sex characters developed, such as the pads on the hind legs and the broad tail. I would wish to dissect a larger series, before drawing definite conclusions about the maturing of the testes. A good series of sections would show whether they are really mature, or not, in the small newt.

In regard to the pits on the sides of the head, I agree with Hilton that they appear in both sexes at or before the time when the red newt enters the water. The two small males which I dissected, however, fail to bear out his statement that the pits appear as soon as the sex can be determined by gross dissection, for neither showed a sign of any pits.

4. If red land newts are kept in a jar of water and no opportunity given to crawl out on land, they soon become completely adapted to water life, with aquatic respiration and ciliated oral epithelium. They also tend to lose their bright red color and to become greenish, although I have noticed that red animals kept for several months in the laboratory generally turn to a darker and duller color, whether kept in moss or water. When first put into water, the newts usually try to climb out and sometimes struggle violently with their narrow tails. I have seen them cling to each other and sink together like drowning men and even float up to the surface half helpless until the water was drawn off to allow them to rest on the bottom. Within a few days, however, they were able to swim well and seemed contented in the water.

Gage ('91b) evidently believes, that, when this adaptation occurs, the animal takes on all the characteristics of the aquatic adult, including the broad, thin edges on the tail. This is probably true, but I should like to prove it by taking careful measurements of several terrestrial specimens of different sizes and watching them closely for several months, after they were adapted to water, to see if the tail really increased in width and length in proportion to the body.

One peculiar thing about this adaptation is that animals which have refused food while kept in moss, will soon eat freely when put into water. I have seen a newt eat a worm in water that it had refused fifteen minutes before on land. None of the twenty-three newts, which I adapted to water at different times, fasted for more than six days after being placed in water, although some of them had refused food for over a month previously.

If bits of earthworm or raw liver are dropped into the jar, the adapted animals will soon begin to nose about the bottom until they find and eat the food, just like the aquatic adults. I believe that this change in feeding is due to a difference in the sense of smell, which seems to be much more pronounced both in the aquatic larvæ and adults than in the land form. This will be discussed more fully later on.

5. Jordan ('93) has grasped an important fact. He says: "One of the first things that strikes the collector of the aquatic form, is the comparative absence of all newts below a certain general grade of development. These young and immature individuals are not to be found in the water by using a net with fine meshes, but may be discovered on land by turning up the stones and logs on the shores of the pond, and one is hence tempted to infer what Gage has concluded, viz: that the red terrestrial form is merely an immature condition of the common aquatic newt." . . .

"I do not yet feel prepared to say that I regard the assumption of the terrestrial habit as a necessary stage in the development of every individual. It is quite possible that certain individuals attain maturity without ever leaving the water, although perhaps the great majority of newts pass their 'Wanderjahre' on land."

The measurement of a large series of animals offers a piece of tangible evidence and this has led me to measure all the specimens available and tabulate the results in graphic form. The courtesy of Dr. W. J. Holland of the Carnegie Museum has made it possible to measure the large series collected by D. A. Atkinson and others. The series in the American Museum of Natural History has also been available through the kindness of Mr. G. K. Noble.

The results of these measurements give a fair survey of the entire life-history of *Notophthalmus*.

Figs. 16 and 17 give the results of all my measurements of total length in the land and water forms respectively. The total length in millimeters is shown on the horizontal line. The vertical lines represent the frequency of the occurrence of any one length. Fig. 16 shows the results of measuring two hundred and eighty-four of the land form from sixteen different collectings, taken at various times and places. The shortest of these measures only 28 mm., while the longest is 100 mm. and the average total length is 62.62 mm. When this is compared with Fig. 17, which shows the measurements of eight hundred aquatic newts representing twenty-nine collectings with minimum and maximum at 71 mm. and 124 mm. and average at 93.05 mm., there can be no further doubt of the fact that the red form is a younger stage of the viridescent. Fig. 16 shows forty-eight individuals or 16.9 per cent. of the total number above 80 mm., and 20 individuals, or 7.04 per cent. above 85 mm.; whereas Fig. 17 shows only thirty-six animals, or 4.5 per cent. of the total number smaller than 81 mm. It looks, then, as if we might take 80 to 85 millimeters as the average length of the terrestrial newts when they re-enter the water to remain for the rest of their lives, and that the variation on both sides of these points is not more than could be expected. With this evidence I feel confident in saying that all newts come out of the water at metamorphosis and that they reach an average length of 80 to 85 mm. before returning to the water.

Fig. 18 gives the same data in a little different form. The entire number was divided into classes according to length, those above 30 mm. and not over 35 mm. with the mean at 32.5 mm. being placed in one class, those over 35 mm. and including 40 mm. in the next class, and so on, while the frequency of individuals in each class is shown vertically. The dotted line represents the terrestrial form and the broken line the aquatic form, while the parallel black line shows total numbers of both kinds. The measurements of aquatic larvæ are not included, for they have not the same significance. They would vary according to age and condition of nutrition from 8.5 mm. at the time of hatching to 28 mm. to 34 mm. at metamorphosis.

The measurements of a large series of animals seems to me the only certain way of telling the exact duration of the terrestrial stage. The two hundred and eighty-four terrestrial specimens, whose measurements appear in Figs. 16 and 18, were collected during every month in the summer from April to October inclusive. Supposing growth to be continuous during the summer and to be stopped completely during the winter, the total length measurements of such a series could be expected to show a straight line, or at least the animals would not be likely to fall into any well marked groups. Fig. 16 fulfils this condition as closely as could be expected. On the other hand, the measurements of a large series taken in one place at the same time, ought to give as many modes as there are years between the time of hatching and the return to aquatic life. My series is too small and was collected at too many different times and places to allow me to draw any exact conclusions. However, I have the measurements of fifty-five animals, collected at Branchville, N. J., in June, 1920, and five more from Amherst, Mass., taken the same month. When these are plotted, as seen in Fig. 19, the newts are seen to fall into three very well marked groups. The first group of fifteen individuals has an average length of 33.93 mm.; the second, taking animals from 42 mm. to 52 mm. inclusive, contains eighteen newts, and has its mean at 46.86 mm., while the third and largest group, containing twenty-seven animals, shows a flatter curve and has a mean of 58.45 mm. Since these groups are so distinct, I feel justified in concluding that they represent animals which are one, two, and three years old. According to this graph, the average growth between the first and second years was 13.51 mm. and between the second and third 11.00 mm. Evidently very little growth takes place after metamorphosis in the fall of the same year that the young newt has hatched, for fourteen newts fall into a well marked group 32 to 35 mm. in length. It will be remembered that the larvæ attain a length of 28 to 34 mm. at metamorphosis, so that, when they show so little increase late in the following June, the young newts must have barely begun to grow. Growth during the second summer is rapid and is a little slower during the third. The curve of the third year is broader and flatter than the first two. This is probably due to the increasing effect of varied environment in retarding or stimulating growth. The fact that there are more individuals in the group is probably because the larger animals are more conspicuous and therefore more likely to be seen, especially by a collector who is not a scientist.

To this graph can be added, with no overlapping, the measurements of the fifty terrestrial or changing animals, collected by Miss Smith Oct. 2, 1921. Of the fourteen taken in the water at this time, seven were distinctly rougher, had narrower tails and most of them were redder than the typical aquatic adult, so that in the making of the graphs they have been placed among the terrestrial newts, although they were evidently just returning to the water. These animals had the advantage of nearly a whole summer over those taken in New Jersey in June, so that they would be nearly a year in advance so far as growth is concerned. The mean length of this group is 79.7 mm., which would show an average growth of 21.25 mm. for the fourth summer. This comparison is of less value than it would be, if all the newts came from the same place, but in the want of better data I give it for what it is worth.

As compared with the other figures, 21.25 mm. seems like a very large growth for a single season. It is nearly twice as much as the 11.00 mm. given for the previous season, and of course it is possible that there is another group with a mode at about 69 mm., representing the fourth summer, while this last one represents a fifth. If such a group existed, I should expect to find some of the New Jersey newts falling into it, and, since there were none in that lot longer than 64 mm., I am inclined to think that all the larger animals had returned to the water either earlier in the same spring or the preceding fall. Since I can find no direct evidence for the existence of such a group, I shall attempt to explain the wide gap between the third and fourth groups in another way.

A series of measurements shows that the tail is decidedly longer in the aquatic adult than in the terrestrial form. To learn more of the nature of this change at the time of the return to water, I measured as large a series as possible of both forms, taking the length of tail to the posterior angle of the hind limb and the length of head and body from that point to the snout. The results of these measurements are shown graphically in Fig. 20 (Pl. XLIX). The newts were divided into groups according to total length as in Fig. 18 (Pl. XLVIII) and the average percentage of the tail to the total length is shown vertically, while the length groups are plotted horizontally. The figures at the left show percentage, while the three rows of figures underneath show the mean length of the class, the frequency and the percentage of the length of the tail to the total length. All of the animals measured were plotted together regardless of their color or maturity.

The tail is seen to be from 48.58 per cent. to 59.82 per cent. of the total length of the animal. A glance at the graph shows a fairly steady increase in the proportional length of the tail, correlated with the growth in total length of the animal. It also shows the tail of the aquatic adult to be decidedly longer than that of the land form.

The only inexplicable thing about this graph, is the decided drop in the class having 102.5 as its mean. From the general contour of the curve, I should expect the tail in this class to average 57 per cent. at least, instead of 54.32 per cent., but, while this average is a little above the average length of tail at the time of the return to water, it is surprisingly low, and somewhat weakens the conclusion which I should otherwise be tempted to draw, that unusually long specimens are merely long-tailed individuals.

It will be noticed that the increase in length of tail is fairly steady until the 72.5 group is reached, when there is a very marked rise to the level of the 77.5 and 82.5 groups, which are followed by another rise. Since we have seen that most of the newts enter the water at the length of about 80 mm., I conclude that the tail increases decidedly in length just before the newt enters the water, followed by a short time when it shows little growth. Then comes another period of growth of the tail, slow at first, but becoming more rapid as the newt grows older. The significance of this will be discussed further on, but it is sufficient now to note that it occurs, and that the growth of 21.25 mm. between the third and fourth groups probably represents increased length of the tail rather than rapid growth of the entire animal.

To clear up this point, a large series of newts of both phases should be collected in one locality, as nearly as possible at the same time, and not only measured, but weighed as well.

A possible explanation of increased growth seen after the time of the return to water, would be the taking up of water by the cells of the body and a consequent increase in size at the expense of specific gravity, somewhat in the same way that rapid development occurs in the young tadpole of the frog, while it is still nourished by the yolk, and growth consists of the imbibition of water and the rapid formation of new cells from material already stored in the body. If it could be shown that there is a storage of food in the fat body which decreases after the return to water, this would seem more probable. As it is, only the collection and weighing of a large series as suggested above, could prove such a theory.

In a short paper, published in 1921, I made the statement that I believed that four years was the probable duration of the sojourn of the newt on land. This statement was made before the complete series of measurements had been finished and the conclusion was too hastily drawn. I would now say that most of the newts enter the water at the end of the fourth summer, when they are three and a-half years old and have reached the length of about 80 mm. Probably some remain on land until the next spring, as Miss Smith has suggested, and possibly a few of them even longer. Figs. 16, 17, and 18 (*Cf.* Pls. XLVII and XLVIII) show so much overlapping, that it does not seem likely that the return to water always occurs at the same age or at the same time of year.

Gage ('91b) believes that the terrestrial form enters the water either in the fall or spring, when the young newts are two and a-half or three years old, but he offers no evidence in support of his belief, except his observations. Most naturalists have done considerable guessing about the time of year when *Notophthalmus* re-enters the water after its life on land. The observations of Dr. Wilder and Miss Smith place it from late August to October, and I feel that their observations supply by far the most satisfactory evidence, which has as yet been published.

The fact that the longest specimens of the terrestrial form are considerably longer than the shortest of the aquatic form has been mentioned. However, these last figures may not be as significeant as they seem, because, out of the seven animals longer than 90 mm., five are from North Carolina, where Brimley ('21) has found that all the newts leave the water in the summer and return again in the fall. For this reason it seems likely that these large land forms are merely adults temporarily adapted to terrestrial life. If all such animals were eliminated, much of the overlapping in the graph would disappear.

The newts collected by Miss Smith, Oct. 2, 1921, were sent to me alive at Portland, Oregon, where they arrived in good condition on Oct. 14. In order to see if they were really returning to the water I put them into aquarium jars with moss in one end and two inches of water in the other, so that they could live either in or out of the water, as they liked. Both lots were fed once or twice a week by putting bits of raw meat or earthworm into the water. This method failed to reach the newts which remained on the moss, and, in order to feed these, I released a culture of *Drosophila* in the jar as often as I could get the flies in sufficient numbers.

The fourteen taken from the water were all put on the moss at first and at the end of two hours nine of them were in the water. These newts soon divided themselves about equally into two groups, those which remained in the water, and those which lived in the moss. The lines of these groups were not rigid, for the aquatic animals often crawled out, as typical aquatic adults will do, and I often saw some of the terrestrial group in the water. Seven of these animals were typically aquatic or transitional, when they were received, and at the time when they were last measured, Dec. 18, 1921, seven of them were typical aquatic adults and were found in the water. The measurements showed so little change since October that no conclusion can be drawn. I can only say that half of these newts taken from the water have been acting like terrestrial animals for the two and a-half months that they have been in the laboratory. The only real sign of change, which I can see, is in the color. When received, one was red all over and three others were reddish or yellowish olive. At the present writing (Jan. 7) all are olive with no sign of red left, though five still retain the bright orange of the belly as contrasted with the pale yellow of the aquatic adult.

The newts taken on land showed more of the expected change. At first almost all of them remained on land, but on Oct. 17, ten of them were in the water, and one pair was mating. These were isolated and the male later extruded two spermatophores. Seventeen of these animals on Oct. 26, were preserved for dissection and six others died about this time. One of these was a gravid aquatic female. On Dec. 1 four of the newts in the water showed all the characters of the typical adult male in the breeding season, clasping pads on the hind legs and broad, finned tails. Mating took place occasionally and still does. By the middle of November this lot was divided into distinct land and water groups like the other. When received, only two of this lot could have passed for aquatic adults. Of the seventeen preserved Oct. 26, three were of the typical aquatic form and so were at least two of those which died at about the same time, while of the twenty survivors on Dec. 21, eight had all the appearance of adults. One is a gravid female and two others have the male sexual characters fully developed. At this date, I found nine animals on land and eleven in the water, with two pairs mating. Three of the newts found in the water could be described as yellowish or reddish on the dorsal side, though none of them were really red. All of the rest, including those found on the moss, were olive above, but those on land were orange below instead of yellow. It will be seen then, that at least eleven of these newts have really changed from the terrestrial to the aquatic form in the two and a-half months during which they have been kept, while the rest have changed color although they are still rough skinned. It seems likely that more will adapt themselves to water before spring. If I can get these animals, which were taken on land, and were really terrestrial forms, to lay eggs, which will hatch into the typical *Notophthalmus* larva, I shall feel that the chain of evidence for the identity of the two forms is practically complete.

It seems very strange that the newts captured on the land should adapt themselves to water more readily than a part of those taken in the water at the same time, and I am at a loss to account for it. However, I am not too ready to draw conclusions from animals kept in the laboratory, where conditions are very different from those in nature. If these newts had been left alone, the coming of winter would have compelled them to hibernate either in the water or on land long before this time, so that it is hardly fair to say that they would, or would not, have entered the water this year, basing conclusions upon their behavior under the conditions of equable temperature and limited food-supply, which obtain in the laboratory.

Occurrence. In a brief paper published in April, 1921, I tried to set forth some of the peculiar features in the distribution of the terrestrial form. From the changes at metamorphosis and from the series of measurements, I am convinced that all the individuals of the species pass through the terrestrial stage, in spite of the fact that they are very scarce in some localities. I quote: "I can go to seven pools or streams within a mile of my home in central Maine and find the water form or the larva at the right time of year, but in all my life I have never seen more than five or six specimens of the land form from that locality.

"In some regions, usually hilly, the land form is very abundant, coming out in large numbers after showers. Is it possible that the nature of the country changes the habits of the animal? Such an explanation does not seem very plausible to me, but I can think of no better." (Pope, '21)

Since I have never been able to find the terrestrial form in any abundance, I do not feel qualified to write very much about its habits. However, through the kindness of Miss Smith, I have the following account of its occurrence and habits in a locality where it is abundant. The first paragraph of this quotation is from Smith ('20b) and the remainder is unpublished.

"Several trips have been made by different members of the Department of Zoology of Smith College to the 'Williams Pond,' on the northwest slope of Mt. Toby in the town of Sunderland, Mass. This pond, formed by the damming of a small branch, is almost a quarter of an acre in surface and from one to two feet in depth... The dam is an unusually good vantage ground for observing and collecting *Notophthalmus viridescens*, which are always present in considerable numbers.

"The land form of *Notophthalmus* is sometimes very abundant in certain regions of Mt. Toby, and at other times, is almost entirely lacking in the same localities. As described in *Copeia* (March 25, 1920) upwards of twenty-five specimens were collected from a certain hollow near the 'Williams Pond' on the western slope of the mountain on Sept. 23, 1917, and thirty-five on Sept. 28, 1919. Some of these had evidently just metamorphosed and the others may have been about to go back into the water at the end of their terrestrial period. At no other times have I known of terrestrial larvæ being found in the vicinity of this pond, (which is always teeming with the aquatic form) although I have searched for them in the late fall and throughout the spring.

"About a mile and a-half from this pond, on the road that skirts Bear's Den Hill, so-called, on its south-east aspect, the land form has been found in phenomenal numbers three times to my knowledge. On a rainy day in May 1915, Dr. H. H. Wilder, in walking along this wood-road, counted over 60 of the scarlet form crawling over the surface of the ground and in May, 1916, and again in 1918, parties from the college, of which I was a member, had similar experiences. In 1916 we found the animals nearly to the top of Bear's Den Hill, a height about 250 feet above the 'Williams Pond' and 450 feet above sea-level. It may be significant that these three trips were made during or immediately after a heavy rain, as diligent searching in this locality at other times has resulted in only a few specimens.

"Although there is no other known breeding place on Mt. Toby, the distance and rough character of the hill between this place and Williams Pond, make it questionable as to whether these animals were bred in that pond. The fact that the terrestrial forms are not found at all times may be because they burrow deeply into the ground and come out of hiding only when it is raining or when they are ready to go back to the water. If, however, as is quite possible, these animals had found their way around the hill from the known breeding place, the fact that they could migrate so far would easily account for the fact that they are so seldom found near the habitat of the aquatic stage in so many localities."

Dr. Chase of Western Reserve, has found the land form nearly at the top of Mt. Monadnock, in Jaffrey, N. H. This mountain rises to a height of nearly 2500 feet above the surrounding country and 3100 feet above sea-level. It is well wooded nearly to the summit, but I doubt if there are any pools above the base of the mountain. There are no natural barriers like the cliffs on Bear's Den Hill, but it seems certain from both Miss Smith's and Dr. Chase's accounts that *Notophthalmus* travels to considerable distances on land from its breeding places, as well as to considerable heights in mountainous country.

The almost total absence of the terrestrial form from localities where the aquatic form is abundant and its disappearance at times from localities where it is sometimes very plentiful, remain riddles as unsolved as the scarcity of the adults of *Ambystoma maculatum* or the total disappearance of the spadefoot toad, *Scaphiopus*.

Pike ('86) says: "The young of the second year sometimes leave the water altogether and secrete themselves in damp places. When droughts occur and the ponds dry up, I have often dug them out, all huddled together more than a foot below the surface, and when the clayey ground has become so parched that they are unable to burrow, they are often seen several together, dead and dried up."

Pike may have the real answer to the question in this paragraph, but it needs confirmation.

Color and Appearance. The general appearance of the land form, even in alcohol, is smoother and plumper than the adult and the coloration is much more uniform. A few black dots appear on the tail, sides, and abdomen, but few or none on the back, while the whole appearance is pale. A land animal is conspicuous in a jar of alcoholic specimens because of these differences in color and markings.

The vermilion spots appear before metamorphosis, but the black borders do not usually surround them completely until the second or third year. The spots on a large red newt are very conspicuous. The brilliant red spot, with a clear ring of jet-black, stands out very sharply on the duller, and otherwise spotless dorsal surface.

The tail is narrow and slender, but decidedly compressed, especially at the tip. While it is far rounder than in the adult, it is not truly cylindrical, as in the case of *Plethodon.*

As has been noted, the color is quite variable. Again I must refer to Gage ('91). "The general coloration of the body is almost always lighter on the ventral than on the dorsal portion and differs greatly in different specimens. In some specimens, it is a bright color in which yellow is very prominent, in others the shade is more red and in still others it is a dingy reddish brown." Fig. 21 is a photograph of two typical red newts.

Other terms used by various writers are: "vermilion," "scarlet," and "pale orange."

Texture of the Skin. Much has been written about the rough skin of the land form as contrasted with the smooth-skinned adult. While there is a real difference between the two, I think that it has been over-emphasized. After the larval period, *Notophthalmus* is distinctly a rough-skinned animal. The adult is never slippery like *Ambystoma* or *Desmognathus.* The fact that the adult is generally wet, makes it appear smoother than the land form and some of them are really quite smooth, but under the binocular the skin of both forms is seen to be covered with fine tubercles or papillæ. These have somewhat the appearance of a volcanic crater, a roughly conical shape with a slight depression in the center where the duct of one of the dermal glands opens to the surface.

In the aquatic form the skin shows considerable variation under the binocular. In some cases, especially those of large, smooth newts, the papillæ stand well apart with broad, flat spaces between them. In other animals the papillæ are set closer, stand higher above the surface of the skin, and the skin itself is more wrinkled between them.

In the land form, this condition is still more marked. The papillæ are larger in proportion to the size of the animal, and, as noted by Gage, are often brown at the tips, while the wrinkles are deeper than in the adult. However, this difference is rather in degree than in kind, and I would hesitate to say that one form is rough and the other smooth.

A cross-section of the skin shows the papilla as a thickening of the epidermis with the duct of a gland opening through it. This gland is large and saccular, lined with nuclei, like the other, more numerous dermal glands, but, unlike them, the nuclei are smaller and more numerous; and the contents of the gland do not stain so deeply with eosin. Possibly it is the secretion of these glands which makes *Notophthalmus* respected by some of its natural enemies.

In order to test the disagreeable properties of the secretion of these glands, I held an aquatic *Notophthalmus* in my teeth for one minute while it struggled. It felt slippery to my tongue, but no taste was perceptible, until two minutes after it was released, when I noticed a slight bitter taste which was not very strong nor very disagreeable and lasted for only a minute or two. The flow of saliva was not noticeably increased. Thinking that the more poisonous part of the secretion might not be discharged unless the animal were strongly irritated, I took the animal again and bit off the tip of its tail, holding the tail in my mouth for a full minute afterward. Irritation seemed to have no effect, for the taste was less strong than before.

It has seemed to me that there must be something disagreeable about *Notophthalmus*, for I have left it in the same aquarium with young pickerel, which would promptly swallow a large minnow, but never offered to touch the newt. Larvæ will be eaten at once by sunfish, minnows, or pickerel, but the adults seem to be immune. The only evidence of natural enemies which I have ever seen, was the occurrence of several newts with the tail gone a little behind the cloaca. Since *Notophthalmus* cannot autotomize its tail, I believe that it was bitten off by some natural enemy, possibly a turtle, or muskrat.

I have been told that garter-snakes in captivity will eat the land form very readily, and it is quite possible that water-snakes and frogs prey on the aquatic adult. To test this, I placed two newts in a large jar, containing an adult green frog, *Rana clamitans*, and three bull-frogs, *Rana catesbieana*, of about the same size as the green frog. In fifteen minutes one of the newts was gone and the other had disappeared at the end of two hours.

Food. Pike ('86) says the food of the land form consists of: "Spiders, insects, earthworms, etc." and believes that the change of food influences the change of color. Gage ('91) gives them the same bill of fare, mentioning insect larvæ in addition. Dr. Parker tells me that he has seen them on Mt. Monadnock, crawling up under a wormy mushroom in the woods to catch the maggots which fell out.

Feeding the red ones in the laboratory was a problem at first. Some will soon learn to take pieces of raw meat or earthworms from the end of a pin but others refuse to eat, even with this painstaking method. A hint from the American Museum led me to try releasing a culture of Drosophila in their jar and then the problem was solved. The movement of the flies attracts them, and while they cannot follow to the top of the jar, they are on the alert to snap up any fly which crawls within reach. Six newts will dispose of one hundred or more flies in an hour or two.

Respiration. The lungs are very much like those of *Necturus*, although they are much longer in proportion to the size of the animal. They are slender and delicate, extending well back into the pelvic region and growing larger at the posterior end. The throat is in continuous, rapid pulsation at a rate that is very variable. Whipple ('06) has timed these throat-movements carefully and found that in different specimens and at different times, they vary from one hundred and four to two hundred and thirteen per minute. These rapid throat-movements serve only to change the air in the mouth and throat in bucco-pharyngeal respiration. This is varied by pulmonary respiration, which Whipple describes:

"As a result of the prolonged depression of the floor of the mouth, air is first drawn in through the open nares, as in bucco-pharyngeal respiration. This part of the process is known as aspiration. During the latter part of the act of depression, however, when the external nares are closed, air is drawn from the lungs into the mouth through the opened glottis and the air in the mouth thus becomes a mixture of pure and impure air. This part of the process is termed expiration. When the floor of the mouth rises again, some of this mixed air is forced into the lungs, the external nares being still closed. This constitutes the process of inspiration. Finally the external nares are opened again, and the fluctuating movements of bucco-pharyngeal respiration are resumed."

The fact that the land form can be made to eat by adapting it to water, has already been mentioned. This might suggest that they sometimes go into the water to feed. The fact that they are often found at some distance from water, makes this seem unlikely, but another explanation seems more probable. As we have noticed, the red newt is seldom seen except during or after a rain. Is it not probable that abundant moisture quickens its sense of smell and that it comes out to feed at such times? If this is so, it does not seem strange that the animals eat better in water than on land.

4. AQUATIC ADULT.

Change in Form and Color from Land Form. Little can be added to what we know of the coloration of the two forms. The change at the time of entering the water may be great or small, according to the color of the terrestrial animal, but there will always be some change, for I have never seen a terrestrial specimen as dark green as the typical aquatic adult. On the whole there is much more uniformity of color in the aquatic adult than in the terrestrial form, although some animals are pale with the black markings over sides and tail forming a very conspicuous pattern.

The color over the back and sides is uniform, dull olive green, frequently quite dark and growing paler on the tail. This dark color ends abruptly at the origin of the limbs so that the upper side of these is green and the under side yellow. On each side, at about two-thirds of the distance from the line bounding the yellow to the ridge of the backbone, is a row of bright vermilion spots surrounded by rings of black pigment. These spots vary in number from three to eight on a side and extend from the head to the inguinal region. They are usually round and about one-half a millimeter in diameter. In addition to these bordered spots some animals show a number of finer red dots, sprinkled irregularly along the sides.

The small black spots, scattered over the back, seem to appear at or soon before the time of going into the water, for the red newt seldom shows them. The under parts grow considerably paler at this time. Instead of the clear, bright orange of the land form, the under parts of the adult are clear, bright yellow, sprinkled with black spots. The size and distribution of these spots is variable. Some females especially, have the abdomen very finely speckled.

The principal change of form is in the tail. In the smallest of the land animals this may be shorter than the combined length of head and body. It grows longer in the larger ones, while in the adult it always exceeds the length of the head and body. Soon after the return to the water it also broadens considerably, developing a fin both dorsally and ventrally. This change is easily explained by the change in function. On land the tail is an unimportant balancing organ, sometimes used as a hook in climbing, but in the water it becomes the principal organ of locomotion. Fig. 20 (Pl. XLIX) shows that the increase in length occurs at two different times; the first is when the land animal is about 75 mm. long, that is during the last summer of its life on land, while the second begins after the newt has entered the water and has had time to establish itself. This is probably the first summer after the return to water, for it begins at the length of 85–90 mm. The flat part of the curve between the two points showing growth may mean that the tail is broadening rather than lengthening just at this time. Width is now more important than length, for a narrow tail is of little use in swimming.

The width of the tail varies with sex and season. In the female the tail is usually narrower than the body, while that of the male nearly equals the width of the body at most times, and decidedly exceeds it during the breeding season.

Respiration. In the aquatic adult, there are two forms of respiration, which might be termed aquatic and pulmonary, corresponding to aerial and pulmonary in the terrestrial form. Copeland ('13) has described the first process accurately:

"Certain intermittent mouth movements of *Diemyctylus* are conspicuous. These consist of a rather slow expansion of the floor of the mouth, followed by a sudden contraction, at which time the mouth is slightly opened. If carmine suspended in water is squirted from a pipette over the snout, it is drawn in through the extended nares as this expansion progresses, and expelled from them and from the mouth, when the contraction follows."

The rate of these throat movements is much slower than in the land form. The rate varies considerably, (from 3 to 23 per minute) according to Whipple ('06) and the amount of expansion is not always uniform. However, these slow oscillations almost always expand the throat more widely than the rapid motions of the terrestrial form. As Whipple ('06) has written such a careful account of aquatic bucco-pharyngeal respiration, including a table showing the frequency of the throat movements in four animals, I shall not allude to it further in this paper.

Once in two minutes on the average, the animal swims to the surface, expels a bubble of air, snatches a mouthful of air with a quick jerk of the neck and then floats passively at the surface or sinks again with all four legs sprawling in the water. Frequently one or two bubbles are set free after the newt reaches the bottom again.

Whipple ('06) describes this act as: "A quick gulping motion by means of which the water in the mouth is replaced by air. This is immediately followed as the head again returns to the water by a forcible swallowing motion as the result of which the air is forced from the mouth partly into the lungs and partly out through the nostrils."

I found that the frequency of this aerial respiration of the adult averaged once in 2.85 minutes. Four experiments were performed in which the animals were watched for thirty minutes and the frequency of taking breath noted. The results are shown in the following table:

Expt.	Respirations	Shortest Interval	Longest Interval
I	11	1.5 Minutes	6 Minutes
II	2	4.5	24.5
III	9	1	9
IV	10	1.5	5.5

To determine whether this pulmonary respiration is essential, I have experimented on several newts by confining them in a wire cage so that they could not reach the surface. When the cage containing a newt was set into a jar of water containing about one gallon, with a control animal in the jar outside the cage, the newt in the cage became very restless within an hour and tried constantly to reach the surface. This continued without much change for several hours and the animal invariably died within ten or twelve hours, while the control animal outside the cage, where it could breathe at the surface, showed no ill effects.

To make sure that death was not due to the exhaustion of oxygen in the water, I confined a newt in a cage in one of my balanced aquaria, where there was no other animal life, but where the plant growth was thrifty enough to supply oxygen for several fishes. Under these circumstances death could hardly be due to lack of pure water. The newt thus confined tried persistently to reach the surface for an hour or so after it was put into the cage but after that showed no signs of discomfort for five days, when it was found dead on the morning of the sixth day.

Whipple ('06) has confined newts in small wire cages in a tank of running water with a specimen of *Necturus* in the jar to keep the air from collecting in the cage. Such animals remained perfectly normal for periods of seven to ten days with no apparent inconvenience, although the capillaries of the skin distended with blood to an unusual degree. Possibly the difference in results may be due to the running water being more heavily charged with air, or it may be that my animal died from some other cause than lack of oxygen, since it is hard to believe that it would have drowned after living for five days.

These experiments and the fact that newts remain more or less active under the ice in winter, lead me to believe that pulmonary respiration is not absolutely necessary to life provided that the water is pure.

Habits. When *Notophthalmus* is kept in the laboratory, it will thrive in any jar or aquarium regardless of depth if kept supplied with food such as raw meat, fish, liver, earthworms, etc. If, however, a stone is put into an aquarium so as to reach the surface of the water, the newts frequently crawl out of the water and sometimes remain for hours with the head and part or all of the body exposed, until the skin becomes quite dry.

At such times aerial respiration is going on, the throat pulsating rapidly in much the same way as in the terrestrial animal. As a rule, the water newt will crawl out of water and remain from five to fifteen minutes before beginning aerial respiration. The newt may or may not open the mouth and gulp at the beginning of this breathing process. Whipple ('06) found that this delay was due to the fact that the nostrils were filled with water, which must be expelled before respiration could begin.

Why *Notophthalmus* should crawl out of the water in this way is not clear to me. I once kept nineteen newts for over a month in a jar ten inches in diameter with three inches of water in it. This water was usually changed once a week and seldom became very foul, though there was probably little oxygen left in it. A pile of stones in the middle gave an opportunity for the newts to crawl out of water, which they did constantly. A record shows that there were always from one to ten newts on the stones all the time, with head or head and body out of water. When the stones were crowded, they climbed over one another to get as high as possible, and then raised their heads straight up into the air like seals on a rock.

I kept a record of the number of newts on the stones each hour of the day between 7:00 A. M. and midnight to see if time of day or conditions of lighting made any difference. The results of this were purely negative, showing nearly the same numbers for any time of day.

One is first led to believe, that, when the water loses its oxygen, the newts take to aerial respiration, but, if so, I would expect a change of water in the jar to make a decided difference. Since I could see no such effect, I doubt if this is the explanation.

I have never seen the aquatic adults out of the water in their natural state. Possibly the light out of doors is too strong, but, if so, they might be expected to crawl up on logs or stones at night, as turtles do in the day time. I have looked for them at night in ponds where they are abundant, but have never seen any out of water.

Notophthalmus is a sluggish animal. It crawls slowly about the bottom or through the weeds of the pond or rests quietly for hours, sometimes coming up for a breath. Even in its feeding habits, *Notophthalmus* is not very active. Much of its prey consists of molluscs, which require no agility to capture, but, even when catching tadpoles or insects, the newt shows so little intelligence or activity, that one is led to wonder how such a blundering creature can catch food enough to live. I have noticed one approaching a school of little tadpoles feeding along the bottom. The newt slowly swam a few inches toward the tadpoles and then stopped. This was repeated three or four times, until it suddenly seized a tadpole that swam close to it. The tadpole struggled violently and escaped, without the end of its tail, alarming the rest of the school and leaving the newt without "a square meal."

I have caught them with a fish-hook, using worms for bait, but not by the usual method. When the hook is held quietly near the newt it will seize the worm and cling to it so tenaciously that it may be lifted out of the water before it will let go.

I have frequently seen *Notophthalmus* in what might be called a state of hypnosis. The body is usually slightly curved and is perfectly rigid and motionless. The head is bent slightly downwards, the tail may be thrown into waves or kept straight, while all four legs are strongly flexed. The eyes may be open or depressed and closed.

In one case I saw another newt swim past and strike the rigid animal, making it drift away passively without a sign of life. This state of hypnosis seldom lasts more than a few minutes, when the newt slowly resumes its normal activities and swims away. I feel sure that this has nothing to do with mating activities, for the two cases studied most carefully occurred in February, when little mating was taking place. Both of these were males, but whether this behavior is confined to that sex, I cannot say.

Occasionally *Notophthalmus* may be seen to yawn widely, opening the mouth to an angle of 90°, expanding the throat to its fullest extent and bending the neck slightly at the same time.

Notophthalmus is not nocturnal in its habits. It may be seen at any time of the day regardless of the sun, feeding, or moving about in shallow water. When taken into the laboratory, it seems to be as active by night as by day.

When kept in a glass jar, the newts have a habit of swimming along the sides of their prison, noses to the glass, pawing at it constantly. If the water is shallow enough, they will raise themselves against the glass and try to climb out of the jar. A theory has been advanced that this behavior was due to the reflections in the glass, that the newt sees its own image and paws at it. I can see no evidence in favor of this, for when the jar is lined with black paper, the animals still persist in their efforts. Furthermore, when a small mirror was left in the jar for two hours, the newts paid no further attention to it than to climb upon it.

The newts tend to gather on the side of the jar towards the light, as though they were positively phototropic. When black paper was first put around the jar, they stopped swimming against the sides for a time, but soon resumed it. When a two inch gap was left in the paper on the side next the window, two newts swam to it at once and began to play back and forth in the lighted streak. During the next hour, there were usually from one to three newts at the lighted side but sometimes it was deserted for several minutes at a time, while half a dozen animals were struggling against the black paper several inches away. From such results, it is hard to believe that phototropism plays any great part in the life of *Notophthalmus*.

Notophthalmus seems to have little if any period of hibernation. Pike ('86) writes: "It may be caught from March to December, as it bears a very low temperature, and I once saw it swimming under the ice in a pond near Fort Hamilton." Gage ('91b) cites both Storer and Holbrook to the same effect. My Pittsburgh records run from March 23 to December 4, at which latter date, Mr. O. C. Wood reports finding them very abundantly. The day was cold after a period of unseasonably warm weather and the newts were lying passively about the pond, apparently stupefied by the cold.

Food. Notophthalmus is essentially carnivorous in all stages of its life-cycle. Its food consists of anything of an animal nature not too large to be swallowed nor too active to be captured. Various naturalists have listed the food of this form.

Pike ('86) says: "Its food is very varied. It will take aquatic and other insects, small tadpoles, worms, especially earthworms, and it will eat small pieces of raw beef and fish when hungry. . . They are very fond of the small, fresh-water bivalves, so abundant in most of the ponds they frequent. Many are swallowed whole; one I dissected had four, shells and all, in its stomach."

Gage ('91) writes as follows: "The food consists of insect larvae, like caddis worms, adult insects, various aquatic worms, earthworms, small crustacea, bivalve and univalve molluscs. In captivity they learn to take bits of meat from a stick, to catch flies thrown on the water and to catch tadpoles."

Jordan ('93) says: "They are exceedingly voracious, and, when freshly captured, almost invariably have their stomachs distended with partially digested prey. They feed chiefly upon insect larvæ and small mollusks, which they swallow bodily. Among the most common objects in the stomachs of the newts are the mollusks, Bythinella, Valvata, Planorbis, and Cyclas; orthopteran and dipteran larvæ; small water-spiders; encased Phryganid larvæ; small crustacea, and the like."

Copeland ('13) made the following report on the contents of a dozen stomachs of newts, which I collected in the early part of August: "Admitting of identification were four snails of two genera, one water boatman (*Corisa*), one caddis-worm, several midge larvæ (*Chironomidæ*) and three amphipod crustaceans."

There is little left to add to this mass of evidence. The bivalves mentioned by Pike are probably *Cyclas*. When several newts are brought into the laboratory and placed in glass jars, they will frequently pass several empty shells of this mollusc. The contents have been digested, but the acids of the stomach appear to have had little effect upon the shell. I once dropped several beetle larvæ, found under stones in a wet place in the winter, into a jar containing some newts. One immediately seized a grub by the tail, when the latter, which was an inch long and armed with a formidable pair of jaws, turned around and bit viciously at the eyelids and other parts of the newt's head. The salamander squirmed in evident pain and used its paws to push away the grub but refused to let go. The grub slowly disappeared, tail first and although I saw blood start when it bit the tip of the newt's lower jaw, it must have settled up its accounts inside.

The method of catching tadpoles employed by *Notophthalmus* has been mentioned already. I have put masses of frog eggs into the aquarium and seen my animals gorge upon them. The jelly makes the eggs hard to swallow but I have seen a salamander literally wade into an egg mass, disengaging and swallowing one egg at a time. Newly hatched tadpoles make even better food and the newts eat them freely.

Habitat. Any pond, lake, or pool, with plenty of water-plants or with marshy shores, or any sluggish stream where conditions are similar, forms a suitable environment. I have mentioned seven stations near my home where *Notophthalmus* can be found. One of these is an abandoned granite-quarry containing a pool of water; two are little marshy ponds, formed by the damming of brooks; another is a sluggish brook, forming broad pools in a field; another a large pool, where muck has been dug; still another the shallow, marshy shore of a lake; and the seventh the mouth of a brook, emptying into Lake Cobbosseecontee. These stations seem quite typical and show a variety of conditions. The quarry is in woods on top of a hill. It contains a pool from three to five feet deep in its deepest part, depending upon the season. As may readily be imagined, the water in such a shallow pool in the rocks grows very warm in the summer. Yet the place is always well stocked with *Notophthalmus* and is also a favorite breeding place for *Ambystoma maculatum.* The location of this pool is interesting also, for it is on the top of a hill at least a quarter of a mile from any other body of water. *Notophthalmus* must have reached it by migration over land while in its terrestrial stage. This quarry is shown in Fig. 22.

I have seen *Notophthalmus* only once in any of the numerous lakes of that part of Maine and that was on a shallow and somewhat marshy shore. Smaller bodies of water seem to be preferred.

Distribution. Notophthalmus is widely distributed throughout the eastern part of the United States. I have collected it in Maine, Massachusetts, Illinois, New Jersey, New York, and Pennsylvania.

Cope ('89) says: "This variable species is the aquatic salamander of the eastern region of North America." He gives a list of specimens in the National Museum captured in all parts of the eastern United States from Connecticut and New Jersey westward to Wisconsin and Illinois, and southward to Louisiana, Alabama, and Georgia, with one collection from St. Catherine's, Canada. Records for the land form, listed separately as *Diemyctylus viridescens miniatus*, extend this range somewhat, including "Hudson Bay," "Upper Mississippi Valley" and "Brazos River, Texas."

Adaptability to terrestrial life. If taken from the water and kept in wet leaves or moss, *Notophthalmus* will live indefinitely. Gage ('91) has noted this, and says: "Furthermore, viridescent specimens from the water have been kept in the air for several months, but there was never any indication of a return to the red garb of the immature form."

I have taken adults out of the water a number of times and kept them for several months. For the first few days they are inactive. They remain in hiding most of the time, the skin looks smooth and sticky and the animal seems to be uncomfortable. After a week or two, the skin grows rougher and drier and the newt has become more active. The tail narrows considerably during this period of adaptation. In a broad-tailed male the thin feather-edges fold over to one side and dry down to the skin on the side of the tail. Such thin parts of the skin seem to die and slough off.

Newts thus removed from the water usually refuse food at first. Out of fifty-one so treated in the course of various experiments, only seven would eat during the first week. In the second week, nine more took food; in the third week seven more began to eat, while two others ate after longer periods. Out of the entire fifty-one there were twenty-six which refused to eat at all while the experiments lasted.

Possibly this refusal to eat at first is due to changes in the mouthparts. The aquatic adult, like the aquatic larva, seizes its food with its jaws, while the terrestrial newt, as noted before, throws its tongue well out of its mouth to capture its prey. After the aquatic adult has become adapted to terrestrial life and has learned to feed, it extends its tongue as far from the mouth as the land form. There must be a decided change in musculature to allow this, so that the delay in feeding may be due to the necessity for these changes in the mouthparts.

It would be interesting to make careful dissections and paraffin sections of the tongue and hyoid region of newts undergoing this adaptation, for I can think of nothing exactly comparable to it. The change in feeding habits seems to occur in response to a change in food correlated with the forced change in environment. In view of this and of the fact that in the South it always comes out of the water in the summer, it appears to me that *Notophthalmus* is a very adaptable animal, and possibly one, which is undergoing an evolutionary change and becoming more terrestrial.

It seems probable to me that this adaptability serves to save the animals in time of drought. It has been noticed that *Notophthalmus* tends to crawl out of the water and breathe air when kept in the laboratory. This occurs at any time of day, but perhaps a little oftener at night.

Let us speculate a little on what may happen when a pool goes dry. As the water becomes decreased in volume and consequently grows foul, the newt may leave it at night, and sit on rocks or the banks. By the time the water is all gone, most of the newts would have become somewhat adapted to terrestrial life by continued exposure to air, and would start off across country at night to look for another pool. This is a mere conjecture, and probably seldom occurs, for most of the ponds or pools where *Notophthalmus* occurs are of a permanent character.

Since the foregoing paragraph was first written, Miss Smith has described such a pond near the "Williams Pond." She says: "It probably is normally fifty yards across, but is now completely dried up and has a pathetic little group of skeletons in the middle of it, where the water last was." Evidently not all of the newts escaped from this pond when it dried up, but it is quite possible that some of them may have done so.

SUMMARY OF LIFE-HISTORY

1. *Notophthalmus* breeds in shallow ponds or sluggish streams from March to July.
2. Fertilization is internal by means of spermatophores; mating serving merely to bring the sexes together and to stimulate them into sexual activity.
3. The spermatozoa are stored in spermathecæ in the dorsal wall of the cloaca of the female, fertilization taking place when the eggs are laid.
4. The pits on the side of the head of the male are lined with glands, which evidently serve to stimulate the female at the time of mating.
5. Mating also takes place in the fall from September to December, although no eggs are laid. This seems to be preliminary to the mating season in spring, for it continues more or less all winter in the laboratory.
6. The eggs are laid singly on the leaves of submerged water-plants, grass, etc. They hatch in twelve to eighteen days in the laboratory.
7. The larva hatches in a very undeveloped condition. It has "balancers" on the head, the fore limbs in the "bud"-stage, and no hind limb buds.
8. The food of the larva consists chiefly of small crustacea with probably some green algæ in addition.
9. Before metamorphosis the color changes from greenish brown with white under parts to the dark olive of the adult with vermilion spots on the sides and yellow abdomen.
10. At metamorphosis the gills are lost, as well as the broad feather-edges of the tail; respiration becomes aerial; the young newt swims with difficulty and comes out of the water, if given the opportunity.
11. The young newt does not become red at once, but remains green for some time, at least in the laboratory.
12. The manner of securing prey changes at metamorphosis from seizing it with the jaws to capturing it by throwing the tongue well out of the mouth after the manner of toads.
13. The terrestrial form is not always red, but varies between that color and a reddish brown, sometimes approaching the green of the adult. Red is the prevailing color of the terrestrial form, but the greenish phase is sometimes found. Color alone is not a constant

character, but varies from brilliant orange to different intensities of olive-brown regardless of sex or season. The olive phase becomes more abundant as the land form approaches maturity.

14. Red animals may be changed to the viridescent color in the laboratory but the opposite change has never been induced. Olive appears to be the more stable color.

15. The terrestrial form is readily adaptable to water and feeds more readily in water than on land.

16. The respiratory movements of the land form consist of a rapid pulsation of the throat varied by occasional larger expansions of the throat and heaving of the sides. Probably most of the respiration takes place in the throat and a little in the lungs.

17. The food consists principally of small insects, larvæ of insects, spiders, and small crustacea. *Drosophila* furnishes a good diet in the laboratory.

18. The skin of the land form is similar in structure to that of the adult, though noticeably rougher, while both are rough as compared with the larva.

19. A series of measurements shows that the newts probably remain on land until they are three and a-half or four years old, when they attain a length of from 80 to 85 mm.

20. The proportional length of the tail increases from the time of metamorphosis until the animal has reached its full length as an adult.

21. The red newt probably returns to water in the latter part of the fourth summer of its life.

22. In the South the terrestrial stage is a seasonal phase, all the newts leaving the water in the spring and returning in the fall.

23. Although all individuals pass through the terrestrial stage, terrestrial newts are extremely rare in some localities, where the aquatic form is abundant.

24. Respiration in the land form is of two types, aerial bucco-pharyngeal and pulmonary.

25. When the newts enter the water at maturity the color changes from red to a dull olive-green on the dorsal side and bright yellow spotted with black on the abdomen.

26. Respiration in the adult is aquatic bucco-pharyngeal and pulmonary by means of air taken at the surface.

27. Pulmonary respiration is probably not necessary to life, for

bucco-pharyngeal and dermal respiration can take its place.

28. In the laboratory *Notophthalmus* will often crawl out of water and remain for hours, changing its respiration to aerial bucco-pharyngeal.

29. *Notophthalmus* is a sluggish animal, diurnal in its habits, and blundering in its feeding.

30. There seems to be little or no period of hibernation for the adult.

31. The food is very varied, consisting of almost any small form of animal life.

32. The aquatic stages of *Notophthalmus* are found in lakes, ponds, or sluggish streams; small bodies of water, where weeds are abundant, being preferred.

33. The range of *Notophthalmus* is quite extensive, from Maine and Canada westward to Wisconsin and southward to Texas and Louisiana.

34. Aquatic adults may be adapted to life on land and kept indefinitely in wet moss; but they usually refuse food at first.

Part II. SENSE OF SMELL.

In 1912 Reese experimented on the aquatic adult of *Notophthalmus* and concluded that: "The olfactory sense is the one mainly used by *Diemyctylus* in recognizing food." Copeland ('13) performed a series of much more careful experiments and found that: "In all likelihood sight is the sense used by *Diemyctylus* in the capture of actively moving organisms; whereas other food located through vision is often recognized as such by the sense of smell."

At Dr. Copeland's suggestion I set out to complete his work by studying the sense of smell in the immature terrestrial form of *Notophthalmus*. It later occurred to me that the sense of smell in the aquatic larva was equally important and that careful work on the sense of smell in all three phases of this unusually adaptable animal might throw some light on the nature and importance of the olfactory sense in amphibians. In this part of the present paper I shall describe the experiments performed on aquatic larvæ, young terrestrial animals, and aquatic adults adapted to life on land (not trying to repeat Copeland's work on the aquatic adult) and shall attempt to show the relation of the sense of smell to the normal activities of the animal.

1. SENSE OF SMELL IN THE AQUATIC LARVA.

Two methods were used in working on the larva: first Copeland's method of the baited bag as used with the aquatic adult; and secondly water shaken up with the normal food of the animal and squirted over the nostrils with a pipette, as was done by both Reese and Copeland.

The method used in the first case was to put the larvæ in a battery-jar four inches in diameter and to suspend two gauze bags two or three millimeters above the bottom and about one centimeter from the opposite sides of the jar. One of these bags was filled with chopped earthworms and the other with earth. The position of these bags was reversed once in ten minutes, so as to bring the bag of earth into the place where the baited bag had been. Ten experiments were performed using four different lots of animals. The presence of the food was recognized in ten seconds to two minutes after the bags had been put into the jar. The young larvæ would begin to search aimlessly with their noses to the bottom, turning this way and that sometimes snapping at random but usually working towards the baited bag. When the bag was reached, it was usually nosed, frequently for half a minute or more and often bitten. The motion of another larva sometimes attracted a newt, after it had been stimulated by the odor from the bag. It would crawl towards the other animal and sometimes seize it by the nose, leg, or tail. In no case was the bag of earth bitten or even approached. The exact record of a typical experiment follows:

Aug. 31, 1916; 9:25 A. M. Bags put into battery-jar containing five larvæ. Bait was noticed in thirty-five seconds by one animal.

9:27. First animal moving slowly toward bait, two others beginning to nose about the bottom.

9:29. All five animals sense food, but only two seem to know where it is.

9:31. All animals turning towards bait.

9:33. All moving toward bait, one snapped at bag.

9:35. Position of bags changed. No attention paid to unbaited bag, though larvæ had just been clustered around baited one, when it was in the same place.

9:38. One approaching the baited bag and another the unbaited one, though not coming very close to it. Four are still in region where bait was.

9:40. Two more starting for baited bag.

9:41. All searching for bait. One started for the unbaited bag and two others followed, approached to within two millimeters, then stopped and turned to one side.

9:45. Two nosing and snapping at the baited bag. One searching in region of the unbaited bag, and nosing bag. Does not snap at it.

9:50. Position of bags changed, animals scattered, none within an inch of where baited bag was put.

9:52. Three animals approaching bait.

9:53. Four animals moving toward bait, one snapped at another. The fifth searching.

9:57. Two constantly nosing bag and snapping occasionally.

10:00. One still nosing bag, others scattered and apparently indifferent, perhaps because odor is diffused through water by this time.

10:02. Three searching near bag, one snapped at another and scattered them.

10:04. One nosed unbaited bag for about fifteen seconds and then left it.

10:10. Position of bags changed. Two animals near bait, but paid no attention to the unbaited bag when it was placed near them.

10:13. Three animals searching aimlessly.

10:19. Four animals remain grouped near the unbaited bag, but pay no attention to it.

10:21. One approaching bait.

10:25. Bags removed. Animals were rather indifferent for the last fifteen minutes of the experiment. Before that there were from one to four near the bait all the time after they had it located.

This experiment and the others made in the same way show two things very plainly; first the recognition of food at a distance and secondly the small part played by sight in the finding of it.

Copeland ('13) believed sight to be an important factor in the feeding reactions of the aquatic adult. He says: "All these tests and subsequent ones, indicate that the approach to an object, edible or inedible, is a visual reaction, and that under the conditions described, if smell plays a part in food recognition, it does so after the animal has discovered and moved to the source of stimulus." And again: "These tests show conclusively that *Diemyctylus* is able to discriminate perfectly between two bags, one containing meat and the other not, and that the food sensing occurs after the bag is approached and before it is snapped at, or taken into the mouth."

The results of my experiments on the larvæ show the reverse to be the case, for, as far as I could judge, it was always the odor diffusing from the baited bag that caused the newt to approach it. The first sign of recognition would be the searching reaction mentioned above, while the approach to the bag was almost always slow and indirect, giving little indication that the animal saw it. The fact that the unbaited bag was nosed twice and approached twice more looks more as if sight were concerned, but certainly it is far less important than in the aquatic adult, where Copeland found the unbaited bag approached nearly half as many times as the baited one. From these experiments, and from watching the young larvæ catch *Cyclops* and *Cypris*, I believe the eyes to be functional only for short distances, and that it is the sight of objects in motion and not the objects themselves, which induces the newt to follow or approach anything, as Copeland found in the aquatic adult. This seems to be true when the larvæ snap at each other.

To see if larvæ would find food quickly, if it were put freely into the jar, I dropped some pieces of finely chopped earthworms into a dish containing nine newts. One minute later three larvæ were hunting within four centimeters of the bait. In two minutes five were hunting and one approaching the bait, snapping occasionally at random and at the end of four minutes the first one had found and eaten a piece of worm.

From this it is very evident that the larvæ can recognize food at a distance when it is not in motion, but they show little intelligence in finding it. If sight were important I should expect the newt to recognize an object, as the adult evidently does, and to approach it, but the larva must nearly touch its nose to the worm before attempting to seize it.

Both Reese and Copeland found that the aquatic adult would snap at beef juice when squirted over the nostrils with a pipette. The experiment described below gave similar results. To make sure that it was not the sight or the motion of the pipette that caused the snapping reaction I first used pure water in the pipette and when the results were seen to be strictly negative, substituted worm-juice prepared by chopping up a large earthworm and shaking up the pieces with a little water and then filtering to remove all mucus and solid particles.

July 5, 1920. This experiment was performed on nine animals collected July 3. I took filtered worm-juice in a long pipette, brought the tip of it carefully within five millimeters of the snout of the newts and forced out the liquid gently. All nine larvæ responded in about two seconds with a little start. One followed and snapped at the pipette and four snapped at random. All began to nose about the bottom of the dish.

One more type of experiment was tried in order to eliminate the visual factor entirely. A thimble of porous paper was set into the jar containing the larvæ, left there several hours and then several cubic centimeters of filtered worm-juice was introduced with a pipette and allowed to diffuse into the water of the dish.

In the first experiment, performed on four larvæ, one recognized the food and began nosing about in three minutes, although it was three centimeters away from the paper-thimble, when the worm-juice was introduced. Two minutes later, a second animal, five centimeters distant, noticed the worm-juice and crawled straight for the paper, nosed it and climbed part way up its side, snapping at it several times. A third began to search in ten minutes and the fourth in fifteen. Two other experiments with different animals gave similar results.

These experiments make me feel that there can be no question of the recognition of food at a distance by some means other than sight. It must be either smell or taste, senses which are not easily distinguished in an aquatic animal. Herrick ('08) says that the significant difference is not in stimuli, but in character of responses. Smell is chemical perception at a distance and the response is approach or retreat. Taste is applied to an object in the mouth and the response is either swallowing or rejection.

If we are satisfied with Herrick's definition, there can be no doubt that it is smell, which causes the young newts to approach the bait. However, there are two possibilities of taste being concerned. First, water is taken into the mouth through the nostrils in bucco-pharyngeal respiration, and, if there are taste-buds in the mouth, I can see no reason why they should not be stimulated. Another possibility is that there are external taste-buds on the head or gills, like those on the barbels and the ventral edge of the tail in *Ameiurus*, and that these may be stimulated by food-substances diffused in the water. This possibility is suggested also by a feeding reaction, which I have seen in the larvæ of *Ambystoma maculatum.* In feeding some larvæ with bits of earthworm held on a pin, I noticed that if the food touched the gills, the larvæ seized it at once. A little experimenting on half a dozen larvæ showed that all reacted in the same way.

In this last instance, and, as I believe, in *Ameiurus* also, the food must actually touch the gills or barbels before it is perceived by the organs, so that they do not function at a distance and could hardly cause the reactions described.

In order to avoid possible confusion with the sense of taste, the nostrils of four animals were plugged with white vaseline and their reactions to worm-juice from a pipette were noted.

To make sure that the animals were reacting normally, they were tested first with clear water from the pipette, to which they gave no reaction, and then with worm-juice. All four reacted actively in fifteen seconds to two minutes. No attention was paid to the pipette; but the animals nosed about the bottom, snapped repeatedly and acted as if they were trying to burrow into the bottom of the dish. They were then taken out of the water, their snouts dried a little with filter-paper and smeared with white vaseline in order to plug the nostrils. They were then put into a dish of fresh water and their reactions tested after they had had time to recover a little, in five to eight minutes. None of the four showed the least reaction to the worm-juice. Another test, made an hour and a half later, gave equally negative results, except in the case of one animal, which reacted at that time, when the vaseline had probably come out of the nostril.

II. SENSE OF SMELL IN THE TERRESTRIAL FORM.

The first work undertaken on this part of the problem was done with an odor stream apparatus at the suggestion of Dr. G. H. Parker. The apparatus used was somewhat like that used by Risser in his work on the toad. Figs. 23 and 24 (Pl. LI) are diagrams of this apparatus. Water is allowed to flow through the siphon from the upper bottle into the lower one, displacing the air in the second bottle and forcing a slow current of air into the odor chamber, C, where it is led almost to the bottom of a vial containing the odoriferous substance used. A pinch-cock served to shut off the current, which was regulated by a screw-cock. From the odor-chamber, air passes upwards through a hole in the center of a plate of glass on which the newt is allowed to crawl. To confine the animal and also to guide it near the source of the odor, an enclosure of wire gauze was made in the shape of a figure-8, with the narrow part about an inch wide. Fig. 24 is a top view of this plate, showing the shape of the enclosure. The apparatus was tested with ammonium chloride by putting a little hydrochloric acid into the bottle and holding an open bottle of ammonia close to the opening in the plate, the white fumes showing the direction of the current of air. When this was seen to be very irregular, an electric fan was placed to one side of the apparatus, so directed as to draw the air across the plate towards the fan. This was found to draw the current of air across the narrow part of the enclosure and to work very satisfactorily. The plate was kept covered with a piece of wet towel paper during the experiments. With an apparatus of this sort, there could be no possibility of sight confusing the results, so that any reaction must be due to smell alone. If positive reactions to food-substances could be demonstrated with such an apparatus, the existence of a sense of smell and its relation to the finding of food would be proved.

Most of the substances, used as food by the newt, have little or no smell to the human nose. A food-substance with an undoubted odor, would furnish the best proof of a sense of smell. The little red dung-worm, *Allelobophora fœtida* was tried, because of its rank smell, when irritated. First the newts were fed with it regularly for some days and after they had had time to become accustomed to it as food, one or two animals at a time were placed in the enclosure, with the current of air passing over the pieces of one or two specimens of *Allelobophora*, freshly cut up and put into the vial.

In the first set of experiments, carried on from Nov. 22 to Dec. 15, 1916, four animals were used. They were put on the plate singly, left for from twenty to thirty minutes and watched closely. Several times the air stream was allowed to pass into the enclosure for some minutes before the vial of chopped worms was added to make sure that there would be no reaction without the odor of food. In these experiments, a circular enclosure of paraffined paper was used instead of the one described as having the form of figure-8, and the electric fan was not used.

In all twelve experiments were performed. The hole in the plate was approached twenty times and the animal showed some response fifteen times. This usually consisted of a pause, sometimes accompanied by a lowering of the head. It was hard to be certain that this was a reaction to smell, as it was so slight, and, furthermore, it occurred a few times when only air was passing through the apparatus. Sometimes the newt reacted in a very decided way by stopping and searching about close to the hole, putting its nose down to the hole or even snapping at it. Such clear reactions occurred nine times in the course of the twelve experiments. In six of these experiments, the newts gave no reaction whatever, so that I do not feel that the results of this set of experiments were conclusive.

After the apparatus had been improved, as shown in Figs. 23 and 24, a second set of experiments was performed with much better results. The same four newts were used, but two of them were put into the enclosure at once and watched for from twenty to thirty minutes as before. The number of times each animal passed through the narrow part of the enclosure past the hole in the plate was noted, as well as the times when it stopped or paused and also the times when it showed an unmistakable positive reaction to the odor of food. A tabulation of these results shows that in the ten experiments, the newts passed close to the opening 129 times, showed some reaction 64 times and gave good positive reactions 38 times. The exact account of one of these experiments follows:

Mar. 21, 1917. Odor of dung-worm.

4:23. P. M. Both animals from dish 3 put on plate.

4:25. No. 2 approached hole, stopped and turned back. Repeated within one minute.

4:27. No. 1 approached, paused and passed on. Repeated within one minute.

4:28. No. 1 approached hole, stopped and nosed it for forty seconds, then put nose into the hole and pushed as if trying to crawl down it, then passed on.

4:30. Came to hole again, stopped, searched about and crawled on.

4:32. Approached and tried to crawl into the hole for a full minute, passed on.

4:34. Came to hole and nosed it for five seconds, searched about for ten more and then turned back.

4:47. Approached, paused, and turned back.

4:50. Came to hole, paused, and went on.

4:36. No. 2 nosed the hole and turned back.
4:39. Repeated the reaction.
4:41. Passed by hole without pausing.
4:45. Climbed out of enclosure.
4:46. Ditto.
4:50. Experiment stopped.

It will be noticed that one animal was much more active than the other, until No. 2 became aroused toward the end of the experiment. However, the behavior of the two animals was quite similar.

It is easy to see how the newts might pause or stop when they came to the narrow part of the enclosure regardless of odor, and in fact they sometimes did so, when only the air-current was passing through, but when a newt stopped, nosed or snapped at the edge of the hole, searched about near it and even tried to crawl down it, I can explain its behavior only on the ground that it was stimulated by the odor coming from the hole and that it was trying to find the food which was the source of that odor.

Irritating Odors. A series of experiments was conducted with the same apparatus, using various strong smelling substances not in any way associated with food. The response to these substances was usually to stop suddenly and retreat or sometimes to hurry past. In general, the results were much clearer than those with the worm.

The reactions to different substances will be discussed separately.

Alcohol 95 per cent. Six experiments. Newts would come up to the hole in plate, stop sharply and usually turn back. Reactions very well marked.

Ether. Three experiments. Results similar to those with alcohol, though not quite so clear.

Chloroform. Six experiments with clear reactions. Animals would usually retreat. Climbed out of enclosure frequently.

Formalin 5 per cent. One experiment. Results not perfectly clear. Newts nosed hole and drew back several times at first and frequently passed by without reacting. Toward the end of the experiment, they became very active and passed back and forth over the hole, paying no attention. Results not clear.

Aqua Ammonia. Four experiments. Responses very clear. Newts would stop with a jerk and retreat. Crossed the center only a few times and then hurried past the hole. Never passed it without showing a response. Animals seemed to learn to avoid the center of the enclosure, for they staid in the ends most of the time by the close of the experiments.

Oil of Thyme. Four experiments. Some clear reactions, but newts frequently passed by regardless of the odor. Oil of thyme is evidently less irritating than other substances used.

Oil of Cloves. Four experiments. Reactions better than with oil of thyme. Responses very clear at first, but before the end of the experiment the newts would evidently get used to the odor and pay little attention to it.

The results of these experiments seem to show that *Notophthalmus* is sensitive to irritating odors, but not necessarily that it has a sense of smell. Most of those substances are irritating and possibly somewhat painful when in contact with the nasal epithelium. Ether and chloroform would probably not be irritating, but their strong odor and physiological effect would be quite enough to explain the reaction to them. It seems to me that little light can be thrown on the normal activities of the animal by working with reagents of this kind, which are never met with in nature. Nevertheless it may be that reactiveness to irritating substances would serve to warn the newt against such disagreeable insects as stink-bugs and bombardier beetles.

Feeding Experiments. The method used in these experiments was to give the newt its choice between its natural food, a piece of earthworm, and a piece of paraffin made to resemble the worm in shape, size, and color. To keep the worm from struggling, it was first killed in hot water. The worm and the paraffin were placed side by side on the floor of the terrarium and attention was called to the two by moving the paraffin with a long needle. When the newt started for the bait, the needle was withdrawn and the worm and paraffin allowed to lie perfectly motionless. The following experiment is typical.

Oct. 25, 1916. Piece of dead worm put into the terrarium and attention called to it by moving a piece of paraffin close by. One of the newts approached and nosed the paraffin but took and swallowed the motionless worm close by. Both of the other newts in the dish did the same.

This experiment was repeated fifteen times with very uniform results. Out of thirty-one experiments, the worm was chosen twenty-five times and the paraffin six times. I found that if the paraffin were kept constantly in motion, the newt would approach and seize it almost at once without stopping to test it by nosing it, and would usually swallow it if allowed to do so. These results are similar to those of Copeland ('13) in working on the aquatic adult. He concludes: "The seizure of a moving inedible object is a reaction probably correlated with the character of the natural food of the newt. In all likelihood, sight is the sense used by *Diemyctylus* in the capture of actively moving organisms, whereas other food located through vision is often recognized as such by the sense of smell."

My observations on the land form agree very well with these conclusions, only I would lay still more stress on the importance of sight. My animals were fed frequently with bits of earthworm held on a needle. Whenever the cover was taken from the terrarium they would begin to move about and usually to crawl toward the experimenter. At such times, the motion of another newt would attract them. Frequently two would approach each other and one would seize the other by the nose, leg, or tail, clinging tenaciously. At any time, they could be diverted from food by the motion of the hand near the terrarium or by another newt. Motion attracts them at once and they act as though they associated it with food, but there is no evidence that they distinguish one object from another by sight. Paraffin will seldom be touched unless it is in motion, but, if it is moved, it will usually be seized and often swallowed.

The fact that a bit of paraffin will be swallowed, suggests that taste cannot be of any great importance in feeding. At the same time, any irritating substance will be rejected promptly. A piece of paraffin smeared with clove oil will seldom be touched even if in motion, but if it is taken, it will be put out of the mouth and the snout wiped on the ground with every indication of discomfort.

From these experiments it looks as though sight were a more important sense than smell in the capture of food. It is easy, however, to see the importance of smell. Many of the small insects and crustacea that form the natural food of the newt, have the habit of feigning death, if disturbed. Supposing that a newt approached and snapped at a sow-bug, *Oniscus*, after being attracted by its crawling. The sow-bug would fold its legs and lie perfectly motionless but the newt would doubtless recognize it as food by its smell amd persist until it was captured. A little experimentation along these lines would be interesting.

It seems to me that there can be little doubt that the reactions described are due to the sense of smell. The parts played by sight and smell are fairly obvious and on land there can be no confusion with taste. It may be said that for absolute proof, the olfactory nerves should be cut or the nostrils plugged and the reactions noted. Under the circumstances, I can see little need of such an operation and furthermore I always feel a little suspicious of the reactions in a mutilated animal.

III. SENSE OF SMELL IN AQUATIC ADULTS ADAPTED TO LAND LIFE.

The adaptability of the aquatic adult has been mentioned in Part I, as well as the fact that the feeding habits change again and resemble those of the land form.

The purpose of the experiments was to determine whether these artificially adapted newts retain their sense of smell in spite of the change. The four newts used in these experiments were taken from the water Nov. 9, 1919, and kept in a terrarium from that time until the experiments were begun, April 23, 1920, about five and one-half months. Most of the work was done by the method already described under the terrestrial form, the choice between a bit of worm and a piece of paraffin. Out of twenty-four experiments on the four animals, the worm was chosen eleven times after the newt had nosed the combination from five to forty seconds. The paraffin was seized four times, and sometimes swallowed. Nine times the newts nosed the combination and passed on in apparent indifference. Twice in the course of one experiment, one of the newts passed over the spot, where a piece of worm had been smeared over the damp paper covering the bottom of the jar. Both times it stopped, lowered its head to within one millimeter of the paper and began to nose around like a hound looking for the scent. This behavior is very suggestive, and, if I had been able to get it often, or from many animals, I should feel quite confident in calling it an olfactory reaction.

The responses of these adapted newts are so much like those of the land form that they require little comment other than to say that so far as appears, the adapted animals resume all the activities of the immature terrestrial animals.

IV. AQUATIC ADULT.

The work of Copeland ('13) on this form was so carefully done that it does not seem necessary to repeat it. His conclusions have been commented on earlier, and it seems sufficient to say here that in their essential points my own observations agree with them.

SUMMARY OF SENSE OF SMELL.

I. AQUATIC LARVA.

1. The larvæ of *Notophthalmus* will respond to food-substances placed in the aquarium, by searching about the bottom and snapping the jaws.
2. This response is not due to sight, for larvæ will snap and search at random when worm-juice is squirted over their nostrils from a pipette, and will gather about a bag or a thimble of paper only if food is inside.
3. When the nostrils are plugged with vaseline, there is no response to worm-juice, showing that the reactions described are olfactory rather than gustatory.
4. Sight is functional at short distances, and is chiefly used to perceive motion, as the capture of small crustacea is evidently a visual reaction.

II. TERRESTRIAL FORM.

1. When the odor of worms is passed through a hole in a glass plate, on which newts are crawling, they will often stop and nose or snap at the edge of the hole.
2. When newts are given a choice between a piece of worm and a piece of paraffin, they will almost always choose the worm, if both are motionless, but will seize and often swallow the paraffin if it is moved.
3. When irritating substances are used in the odor stream apparatus, the newt backs away sharply.
4. The reactions described cannot be due to either sight or taste and hence must be olfactory in their nature.
5. The motion of the hand or of another animal will always divert a newt from food. Sight appears to be far more important than smell in the finding of food, but smell is useful in recognizing food-substances when there is no motion.

III. AQUATIC ADULTS ADAPTED TO LAND LIFE.

Experiments with a worm and piece of paraffin gave the same results as in the typical terrestrial form.

IV. WATER ADULT.

The sense of smell in this form has been so well proved by Copeland that further work seems unnecessary.

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